Pacific Hake

Marine Fisheries
REVIEW

On the cover:
Top: a Pacific hake
at 290 m depth at the
western flank of Heceta
Bank, off Oregon, photo-
graphed by W. Wakefield, NMFS.
Bottom: a catch of Pacific hake being
dumped into a commerical fishing vessel,
photographed by M. Wormington, NMFS.

Articles   69(1–4), 2007

Pacific Hake, *Merluccius productus*, Autecology: A Timely Review

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Introduction

The Pacific hake (*Merluccius productus* Ayres 1855, also known as Pacific whiting), a gadoid species inhabiting waters off the west coast of North America (Fig. 1), is the most abundant groundfish in the California Current Large Marine Ecosystem (CCLME) (Sherman, 1991). The biomass of the coastal stock (fish age 3 and older which are susceptible to exploitation) was most recently estimated at 2.5 million metric tons (t) (Helser and Martell,

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2007) (Fig. 2, top) and has supported average commercial landings of about 0.2 million t between 1966 and 2005 (Helser et al., 2006). The Pacific hake fishery currently has an annual landed value of about $22 million in the U.S. and about $14 million in Canada (values in U.S. dollars).[1,2] The commercial catch is mostly processed into surimi, headed and gutted products (Sylvia, 1995), and fillets (Helser et al., 2006), but it has also been used experimentally in such food products such as fish sauce (Lopetcharat and Park, 2002) and even hot dogs (Park et al., 1978).

Ecologically, Pacific hake play a dominant and key trophic role in the CCLME both as predator on euphausiids such as *Euphausia pacifica* and *Thysanoessa spinifera*, shrimp such as *Pandalus jordani*, and smaller finfishes such as the Pacific herring, *Clupea harengus pallasi*, and as prey for other

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[1]NMFS. 2004. Annual commercial landing statistics. Online at http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html.
[2]Fisheries and Oceans Canada. 2004. Commercial catch statistics. Online at http://www.pac.dfo-mpo.gc.ca/pages/data_e.htm)

Pacific hake, larger finfishes such as lingcod, *Ophidon elongatus*, large invertebrates such as Humboldt squid, *Dosidicus gigas*, seabirds such as the sooty shearwater, *Puffinus griseus*, and marine mammals such as the California sea lion, *Zalophus californianus californianus* (Livingston and Bailey, 1985; Buckley and Livingston, 1997; Baraff and Loughlin, 2000; Field et al., 2007).

Population reconstructions based on analysis of fish scales preserved in sediment cores show that the Pacific hake has been an abundant species in the CCLME for thousands of years (Soutar and Isaacs, 1969; Tunnicliffe et al., 2001), but it has been studied and monitored intensively only since the 1960's (Alverson and Larkins, 1969), when a directed fishery began to develop. The long-term potential yield of Pacific hake depends upon its response to climate change and its role as both predator and prey (Methot and Dorn, 1995) in the CCLME.

Previous reviews (Best, 1963; Alverson and Larkins, 1969; Bailey et al., 1982; Stauffer, 1985; Methot and Dorn, 1995) described the incremental increase in the state of knowledge of

ABSTRACT—Pacific hake, Merluccius productus, *the most abundant groundfish in the California Current Large Marine Ecosystem (CCLME), is a species of both commercial significance, supporting a large international fishery, and ecological importance, connecting other species as both predator and prey. Coastal Pacific hake migrations are characterized by movements between northern summer feeding areas and southern winter spawning areas, with variations in annual abundance, distribution, and the extent of these movements associated with varying climate-ocean con-*

ditions. In general, warm (cool) years with enhanced (reduced) stratification and poleward (equatorward) transport are often related to good (poor) recruitment, increased (decreased) northward distribution, and reduced (enhanced) growth. However, the classic periodic pattern of annual migration and distribution may no longer be fully representative. Based on recent advances in the understanding of climate-ocean variability off the U.S. west coast, we hypothesize that the annual movements of Pacific hake are more responsive to climate-ocean variability than previously

thought, and further, that changes observed in Pacific hake distributions may reflect long-term changes in climate-ocean conditions in the CCLME. Therefore, an updated model of these relations is key to effective monitoring and management of this stock, as well as to devising scenarios of future change in the CCLME as a result of climate variations. The current state of knowledge of the relationship between the Pacific hake and its environment is reviewed, highlighting emerging ideas compared to those of the past, and priorities for future research are suggested.
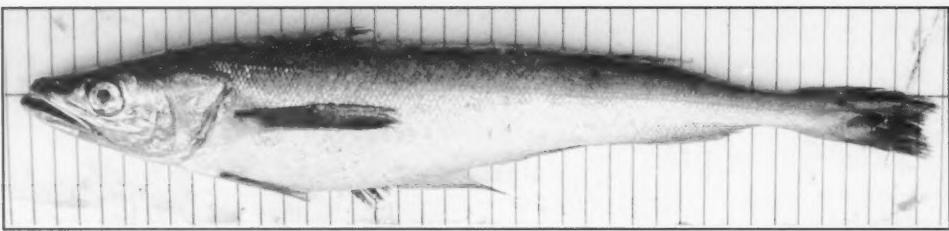
Figure 1.—Photo of an adult Pacific hake, *Merluccius productus*, which generally range from 35–75 cm in length. Photo by Dan Kamikawa, NMFS, Northwest Fisheries Science Center, Newport, Oreg.
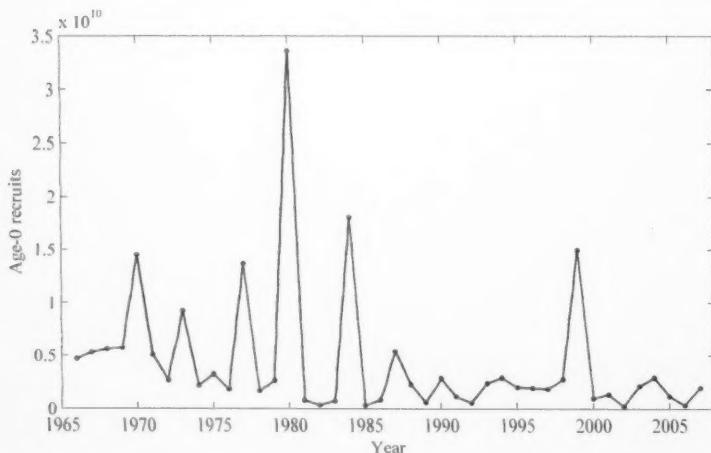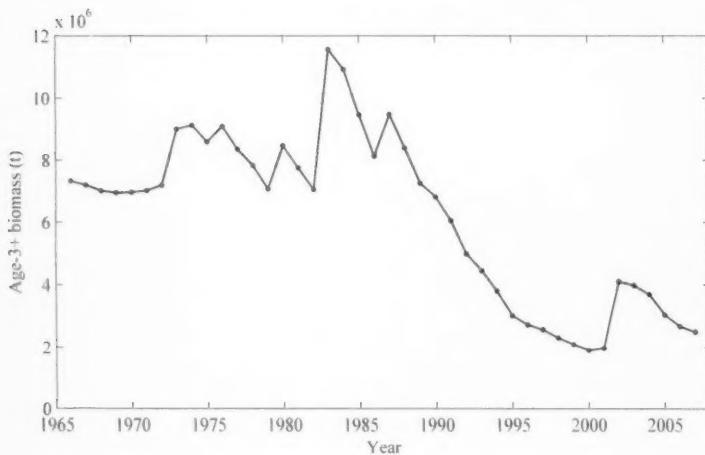
Figure 2.—Model estimated age 3+ biomass trajectory (in metric tons, top) and recruitment time series (in number of age-0 recruits, or the number of hake that survive their first year of life, bottom). From the most recent Pacific hake stock assessment (Helser and Martell, 2007).

Pacific hake at key times in the expansion of the commercial fishery and contributed to the fishery's rapid development since the 1960's. In the 28 year history (1977–2005) of the acoustics-trawl survey used to monitor the coastal hake stock, the ability to observe the fish has improved through advances in equipment and techniques, and our collective scientific understanding of the large influence of climate-ocean variability on marine species within the CCLME has increased. Since changes in climate-ocean conditions affecting the Pacific hake are likely to continue, there is a particular need to understand and devise scenarios of anticipated responses by such ecologically and economically important species. Neither the distribution nor the availability of the stock to resource monitoring surveys is known *a priori* and this uncertainty poses an obvious sampling issue for fisheries management in light of expected trends in oceanic and atmospheric warming (e.g. see Field et al., 2006a) in the foreseeable future. In this paper we review the main aspects of Pacific hake autecology, with an emphasis on the adult life stage, in order to identify key environmental relationships and associated biological mechanisms. Understanding physical processes in the CCLME is crucial to understanding the abundance and distribution of Pacific hake and to inferring how these fish are important indicators of the dynamics of the CCLME. We also highlight recent work on this topic and suggest the main directions for needed future research.

Pacific Hake
Autecology Overview

Zoogeography, CCLME Dynamics, and Habitat

Pacific hake are widely distributed along the Pacific west coast of North America from Baja California to southeast Alaska (Alverson and Larkins, 1969; Dark et al., 1980; Bailey et al., 1982; Saunders and McFarlane, 1997; Wilson et al., 2000; Fig. 3). Three biologically and genetically distinct stocks are now recognized: a predominant coastal stock that migrates annually between southern California (lat. 25°N) and Queen Charlotte Sound (lat. 55°N), and two more restricted populations within Puget Sound and the Strait of Georgia (Iwamoto et al., 2004). Previously, a fourth "dwarf" Pacific hake stock had been recognized in the south off Baja California, but these fish are now considered a separate species (Vrooman and Paloma, 1976; Ermakov, 1982; Mathews, 1985; Grant and Leslie, 2001; Iwamoto et al., 2004). This review focuses on the migratory coastal stock of Pacific hake, which is a major biological component of the CCLME.

Well offshore of the western North American continental shelf break, a broad equatorward flow known as the California Current exists year round. However, along the shelf and slope off Washington, Oregon, and California, predominately northerly wind stress between April and September (summer) drives coastal upwelling and meandering equatorward surface flow, while southerly, downwelling-favorable winds and poleward flow prevail during the remaining (winter) months (Hickey, 1979; Huyer, 1983; Hickey, 1989a; Thomson et al., 1989; Strub and James, 2000; Fig. 4, top). Some poleward flow does occur close to shore during the summer, particularly west of Vancouver Island, B.C., where equatorward surface flow is mostly restricted to the outer shelf and slope (Thomson et al., 1989). In addition, jets, eddies, and filaments are common, especially in late summer and fall (Thomson et al., 1989; Huyer et al., 1998; Barth et al., 2000; Strub and
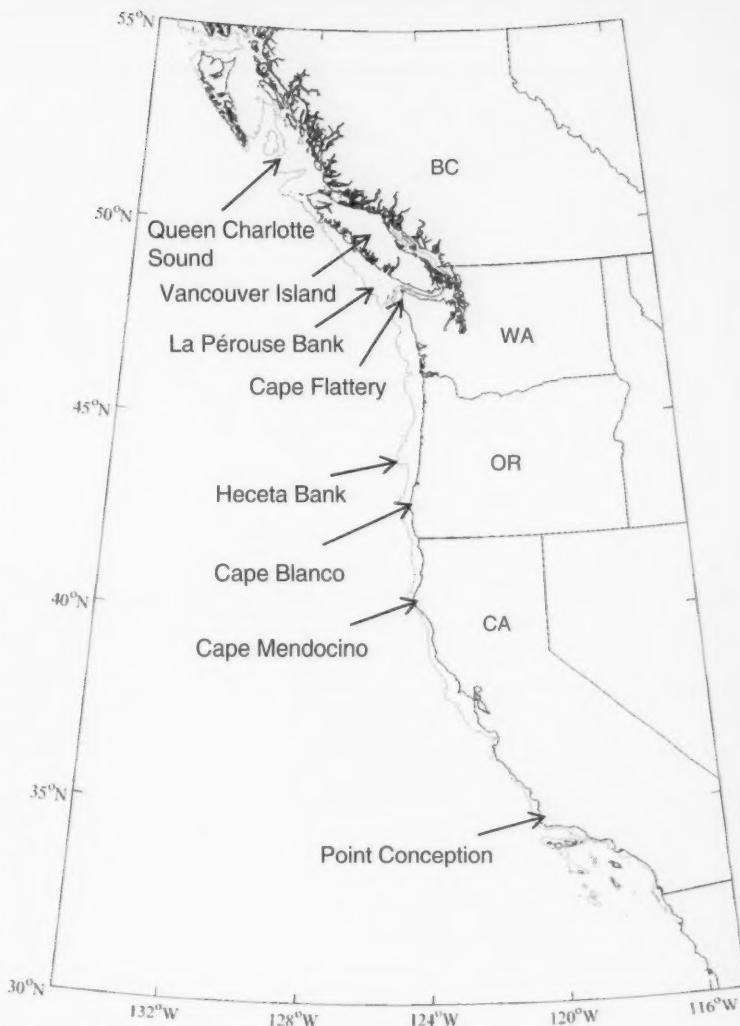
Figure 3.—Pacific coast waters inhabited by Pacific hake, showing physiographic and topographic features mentioned in the text. The 200 m depth contour (in gray) defines the continental shelf break.

James, 2000; Fig. 4, top). During the winter months, the poleward Davidson Current dominates flow over the shelf and slope north of Point Conception. A subsurface poleward flow known as the California Undercurrent exists on the shelf and upper slope year-round (reviewed by Hickey, 1989b; Huyer et al., 1989; Thomson et al., 1989; Pierce et al., 2000; Fig. 4, bottom). The Undercur-

rent is nearly contiguous from lat. 33° to 51°N, with a relatively narrow core (10–20 km) at depths of 200–300 m where mean sustained velocities of 10 to 20 cm s^{-1} have been recorded (Pierce et al., 2000).

Summer upwelling brings cool, dense, and nutrient-rich surface waters to the surface along the coast (Huyer, 1983; Hickey, 1989a), and the combi-

nation of Ekman transport, persistent, strong winds, and flow-topography interactions can draw this water many kilometers from shore (Huyer, 1983; Barth et al., 2005). Off California, the upwelling is relatively steady during the summer, but off Oregon and Washington it is usually episodic, with upwelling events lasting from days to weeks followed by periods of relaxation (Huyer et al., 1979; Huyer, 1983; Barth et al., 2000). In contrast, upwelled water rarely reaches the ocean surface off the west coast of Vancouver Island, because of the stabilizing effect of the large volumes of freshwater discharged from coastal rivers, but the upwelling is sufficient to bring nutrient rich waters into contact with the turbulent mixed surface layer (Thomson et al., 1989). These upwelling circulation and current patterns increase the CCLME's biological productivity (Mann and Lazier, 1996; Batchelder et al., 2002) and are the likely bases for the development of favorable feeding areas for Pacific hake during the summer months.

The fall transition from summer to winter conditions usually occurs in October, when storm events bring a reversal from prevailing northerly winds to southerly, downwelling-favorable winds and the appearance of the Davidson Current (Huyer et al., 1979; Thomson et al., 1989). The spring transition from winter to summer conditions occurs over a period of several days, as the return of northerly winds brings upwelling favorable oceanographic conditions and equatorward flow.

Long-term observations of wind, sea-level, and temperature observations indicate that the spring transition takes place earliest off northern California and propagates northward to British
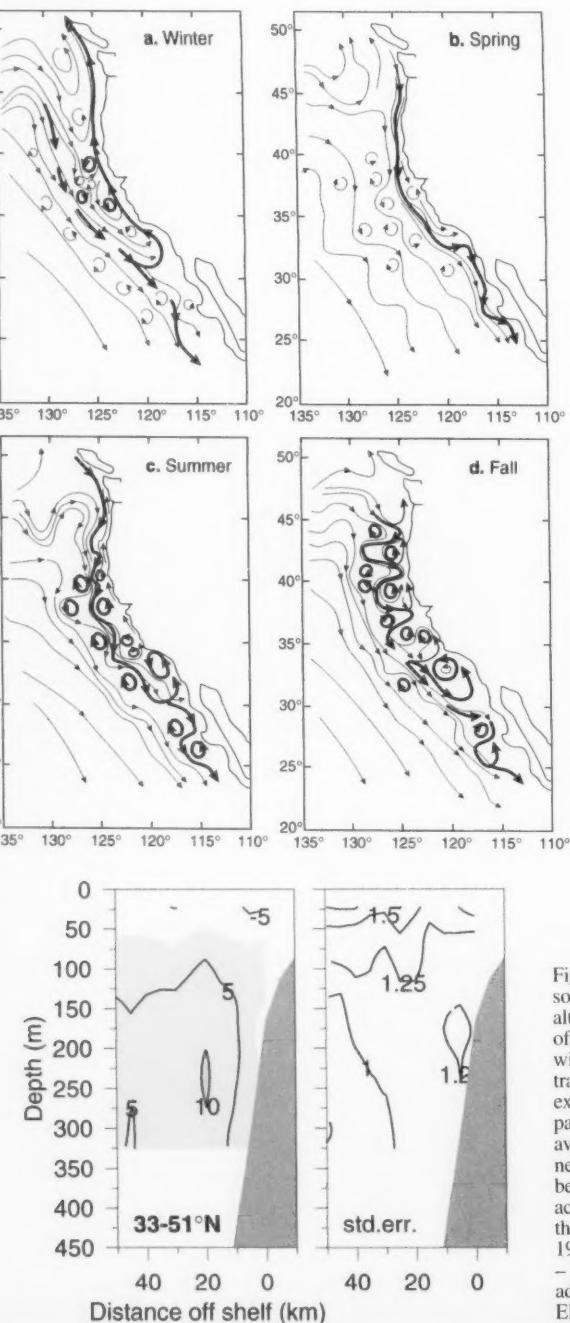
Figure 4.—Circulation in the CCLME. Conceptual drawing of seasonal evolution (top) based on the literature and analysis of satellite altimetry data, reprinted from Strub and James (2000), courtesy of Elsevier. Note prevailing poleward flow on shelf and slope in winter (a), and prevailing equatorward flow between spring and fall transition (b–d.) Seaward of the shelf and slope, equatorward flow exists all year. Meanders and eddies are superimposed upon broad patterns, particularly during summer and fall. At bottom, coastwide average velocity section showing equatorward flow (negative) near the surface and the poleward (positive, shaded) undercurrent beneath during summer 1995. This velocity section is based on acoustic Doppler current profiler (ADCP) data collected during the 1995 acoustics-trawl survey for Pacific hake (7 July–28 Aug. 1995). The depth range for this average section is from 22 m to 125 – 325 m, depending on bottom depth. See Pierce et al. (2000) for additional details. Reprinted from Pierce et al. (2000), courtesy of Elsevier, which gives additional details.

Table 1.—Life history intervals and defining morphological features in the ontogeny of teleost fish (adapted from Balon, 1975).

Interval	Start	End	Characteristics
Embryo	Fertilization	Absorption of the yolk-sac after hatching; exogenous feeding begins	Endogenous nutrition
Larva	Exogenous feeding begins	Formation or ossification of axial skeleton and fins fully differentiated; definitive organs developed	Exogenous nutrition, some embryonic organs
Juvenile	Axial skeleton ossified, fins fully differentiated, temporary organs replaced with definitive organs	First maturation of gametes	Rapid allometric growth
Adult	First maturation of gametes	Last maturation of gametes	Sexual maturity, spawning behavior
Senescent	Last maturation of gametes	Death	Arrested growth, gametes inferior or not produced

Columbia in about one week's time, usually between early February and late April (Thomson et al., 1989). However, the development of strong upwelling conditions is not always coincident with the spring transition, because their appearance is dependent on the strength and persistence of upwelling favorable winds over the continental slope. For example, in 2005 the spring transition off Vancouver Island occurred in late April, but persistent upwelling did not develop until late July[3] after the development of strong upwelling favorable wind stress in the northern California Current (Pierce et al., 2006; Fleischer et al.[4]).

Despite the aforementioned seasonal variability of the marine environment in the CCLME, climate forcing at interdecadal (e.g. regime shifts) and interannual time scales (e.g. El Niño/La Niña events) has also been identified (McFarlane et al., 2000; Benson and Trites, 2002; King, 2005). At present, regime shifts are only detectable retrospectively on the basis of coincidental changes in the distribution, survival, and abundance of many marine plankton and fish species (King, 2005). These changes are relatively abrupt, widespread, and may persist for decades, with effects cascading through all trophic levels in marine ecosystems.

Historical records provide evidence of regime shifts affecting the North Pacific in 1925, 1947, 1977, 1989, and most recently, 1998 (King, 2005). Ocean conditions in the CCLME after the 1998 regime shift can be summarized as a return to cooler, less stratified, and more biologically productive conditions with enhanced southward flow of water and organisms (King, 2005). Within these regimes, ocean conditions are affected by El Niño events, which generally result in a warming of coastal waters over the continental shelf and stronger poleward flow in the CCLME, and La Niña events, which couple cooling of surface temperatures with reduced poleward flow. In both cases, the impact of these events is measured relative to the existing ocean regime; hence no two El Niño or La Niña events will produce identical biological responses to organisms such as Pacific hake.

A warming trend during the late 20th century has been detected in all global oceans and accounts for a 1°C increase in average annual water temperature in the CCLME over the past 50 years (Palacios et al., 2004; Di Lorenzo et al., 2005). Based on abundances of tropical/subtropical (warmwater) and temperate/subpolar (coldwater) species of planktonic foraminifera shell casings in sediment cores from the Santa Barbara Basin, Field et al. (2006a) demonstrated that this recent warming trend is atypical of environmental variability in the CCLME during the preceding millennium and concluded that it represents a signal associated with anthropogenic warming, likely related to increases in atmospheric greenhouse gas concentrations since the late 1880's. This warming is likely to have widespread consequences for

the CCLME, including the spawning, recruitment, abundance, and distribution of the coastal Pacific hake stock.

In the following sections, we follow the general terminology conventions for fish life history intervals recommended by Balon (1975) (Table 1). For Pacific hake, the embryonic period lasts approximately 5–9 days after fertilization, but some exogenous feeding may occur before the yolk is fully absorbed; hake are 2.5–3.0 mm in length at this time (Bailey et al., 1982). The subsequent larval period lasts until about 20 days after fertilization, when the juvenile period begins with the onset of rapid growth (Bailey et al., 1982). Time until entry into the adult period is variable. At fork lengths of 37–40 cm and an age of 3, 50% of a Pacific hake cohort in the coastal stock is reproductively mature (Best, 1963; Methot and Dorn, 1995; Helser et al., 2006). It is uncertain when senescence might occur for Pacific hake, but it is known that they can live for more than 20 years (e.g. Fleischer et al., 2005), though hake older than about 15 years are very scarce (Methot and Dorn, 1995). The natural mortality rate for Pacific hake has been estimated at 0.20–0.30 year⁻¹ (Dorn, 1996; Helser et al., 2006).

Embryos, Larvae, and Juveniles

Pacific hake eggs are spawned from January through March at depths of 100–500 m; the fertilized embryos and larvae remain beneath the mixed layer (Bailey, 1982). Classically, spawning was thought to occur in dense aggregations several hundred km offshore of southern and Baja California (Alverson and Larkins, 1969). However, indirect evidence of successful spawning north of this region has occasionally been

reported over the years (Bailey, 1980; Pearcy and Schoener, 1987; Hollowed, 1992; Dorn, 1996; Saunders and McFarlane, 1997; Benson et al., 2002). Spawning aggregations have seldom been observed directly (Alverson and Larkins, 1969; Nelson and Larkins, 1970; Bailey et al., 1982; Stauffer, 1985; Saunders and McFarlane, 1997; Saunders et al.[5]). Most of what is known about Pacific hake spawning has been inferred from collections of embryos and larvae during standard California Cooperative Oceanic Fisheries Investigations (CALCOFI) ichthyoplankton surveys (Bailey, 1981; Hollowed, 1992;

Horne and Smith, 1997; Mullin et al., 2000).[6] The gear used in the CALCOFI surveys (typically ring or bongo nets with 0.505–0.550mm mesh; Hollowed, 1992) may be inefficient for this species (Hollowed and Bailey, 1989). Other problems with these surveys include a reduction in spatial coverage over the years and difficulty in adequately sampling the apparently patchy and variable distribution of embryos and larvae both within and between years (Hollowed, 1992).

As they grow, juvenile Pacific hake evidently move inshore from offshore areas where they were spawned to develop on the continental shelf and slope (Bailey, 1981; Grover et al., 2002). Juveniles have been collected in midwater trawl surveys by the California Department of Fish and Game (CDFG) (Bailey, 1981), in juvenile rockfish surveys conducted by the NMFS Southwest Fisheries Science Center (SWFSC) (Grover et al., 2002), and more recently in a joint survey initiative targeting Pacific hake and rockfish (*Sebastes* spp.) young-of-the-year juveniles conducted cooperatively by the NMFS Northwest Fisheries Science Center (NWFSC) and the Pacific Whiting Conservation Cooperative (PWCC) (referred to herein as the NWFSC-PWCC pre-recruit survey) (Phillips et al., 2007). Despite acknowledged difficulties (Hollowed, 1992) with surveys of embryos, larvae, and juveniles (Fig. 5), these data are still viewed as potentially useful indices of the strength of recruitment in Pacific hake stock assessments (Helser et al., 2006), as described further below.

Episodic strong year classes, varying as much as over two orders of magnitude (Bailey and Francis, 1985; Methot and Dorn, 1995), characterize the coastal
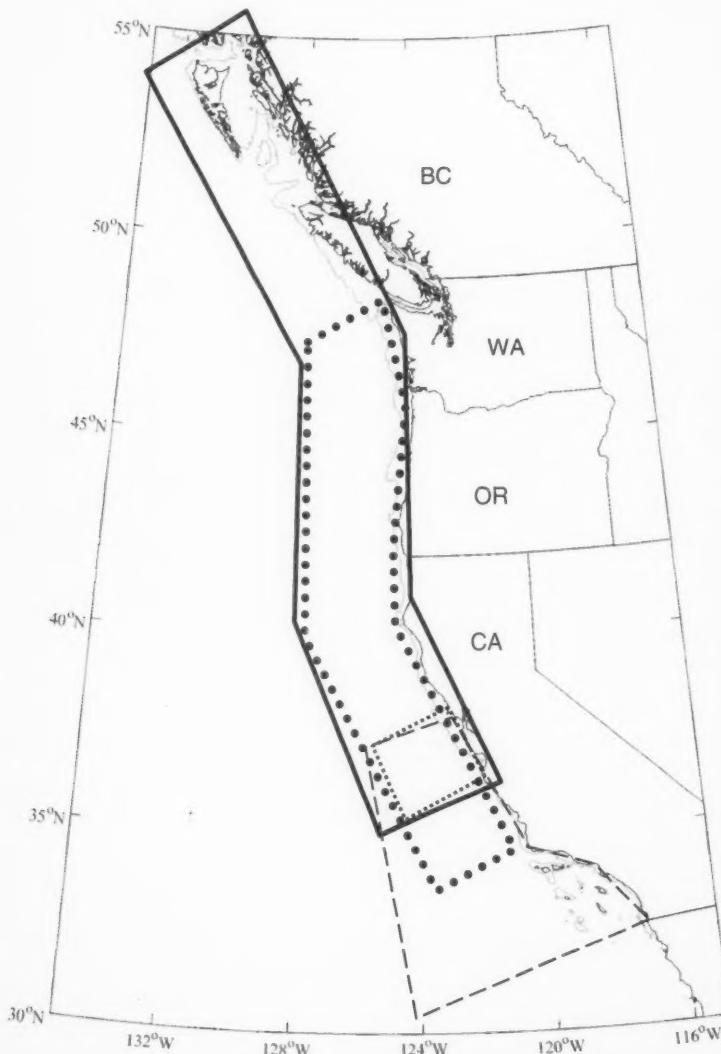
Figure 5.— Current spatial coverage of major monitoring surveys for Pacific hake: acoustics-trawl survey for adults (solid), NWFSC-PWCC survey of prerecruits (dot), SWFSC of prerecruits (short dash), and CALCOFI larval surveys (long dash). The area covered by the surveys has changed over the years. The 200 m depth contour (in gray) defines the continental shelf break.

[5]Saunders, M. W., K. Cooke, M. Wyeth, G. A. McFarlane, and V. Wespestad. An echo-integration-trawl survey of pelagic fishes off the west coasts of Canada and the United States from January 10–February 6, 2001. Unpubl. rep. contact Ken Cooke, Fisheries and Oceans, Canada, Pacific Biological Station, Nanaimo, BC, V9T 6N7, Canada.

[6]NMFS, Southwest Fisheries Science Center. Pacific Hake Larvae Abundance and Spawning Center. Contact Richard Charter, SWFSC, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508. Online at http://test.parsus.com/NOAA/Hake/.

stock of Pacific hake (Fig. 2, bottom). These periodic strong recruitment events promote non-monotonic changes in stock abundance and subsequent harvest levels—typically resulting in periods of increases in both for several years followed by decline until the next strong recruitment event occurs.

Pacific hake recruitment fluctuates largely independent of spawning stock size, so a reliable stock-recruitment relationship, the fundamental relationship typically used to formulate harvest recommendations, has been difficult to establish (Bailey and Francis, 1985; Helser et al., 2006). Varying levels of mortality during the pre-recruit period is a common explanation for this observation in other species, and considerable research has provided evidence that the survival of larval Pacific hake is strongly influenced by the environmental conditions (such as upwelling, advection, and water temperature) experienced during the first few months after spawning (Bailey, 1981; Bailey and Francis, 1985; Bailey et al., 1986; Hollowed, 1992; Agostini, 2005). Cold ocean years often produce weaker year classes, while warm ocean years often produce strong, albeit more variable, year classes. Cold ocean years along the west coast are characterized not only by low water temperature and slower development rates for hake embryos and larvae, but also by stronger upwelling, equatorward transport, and offshore advection (the opposite conditions prevail in warm years). The mechanism for depressed Pacific hake recruitment in cooler years is not clear: it may be advection of embryos and larvae to unfavorable habitat, or the presence of different zooplankton prey and/or predator species brought in by advection during cooler years (Bailey, 1981; Hollowed, 1992; Agostini, 2005).

Although the biological mechanisms affecting recruitment in Pacific hake are not completely understood, most of the available evidence is consistent with the notion that the number of fish that survive to join older age classes and the fishery is strongly influenced by mortality during the first year of life. For example, Bailey et al. (1986) showed

that incidental catches of young-of-the-year (age 0) Pacific hake in CDFG pelagic fish surveys could be useful in forecasting the expected strength of year classes as they become vulnerable to fishing. Although juvenile catches may provide a useful index of year-class strength, Bailey and Francis (1985) and Hollowed (1992) argued that the strength of a year class may already be determined by the time the members of that class reach the juvenile stage, and that predatory and competitive forces at the juvenile stage are probably less important to recruitment than success at the larval stage.

Hollowed and Bailey (1989) contended that, as with Pacific hake larvae, high abundances of juvenile Pacific hake characterize strong year classes, and low juvenile abundances characterize weak year classes. Most of the interannual variability in recruitment was explained by density independent environmental factors. Hollowed and Bailey examined sea level, sea surface temperature, the depth of the 14°C isotherm, upwelling intensity, and temperature at 100 m from measurement stations and model data along the southern California coast and found that recruitment was higher when the 14°C isotherm was depressed and surface temperatures were higher than 15°C, both conditions that would characterize warm years with weak upwelling. Weak upwelling in January or February followed by strong upwelling in March led to stronger year classes. They proposed that Pacific hake larvae reach favorable habitat near the coast by the end of January during years with low upwelling and weak offshore transport. Subsequently, when upwelling increases later in the year, these larvae are protected from offshore transport and are able to take advantage of the upwelling-driven biological production that results. This conceptual model, which was a modification of the model originally presented by Bailey and Francis (1985) using a longer time series, was better able to explain variability in Pacific hake recruitment. Of course, there have been exceptions: 1999, an anomalously cool year in the CCLME (Schwing and Moore, 2000), produced

one of the strongest year classes since the late 1980's (Fleischer et al., 2005; Helser et al., 2006).

Hollowed et al. (2001) reviewed and analyzed patterns in northeast Pacific fish stock and climate index time series. Apropos of the present review, these authors found that Pacific hake (as well as other important gadoids in the Gulf of Alaska, walleye pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus*) appeared to respond more strongly to interannual variability than to decadal climate variability, and they had a statistically higher proportion of strong year classes in unusually warm years than in other years. This result is not inconsistent with previous studies. They defined warm years not on the basis of low latitude El Niño phenomena, but on so-called "Niño North" conditions indicated by warm surface temperature anomalies in coastal waters north of the tropics. Niño North conditions did not always correspond to El Niño events. The frequency of favorable ocean conditions for recruitment has major implications for the size and variability of this stock, as years of strong recruitment store sufficient biomass to ensure survival during periods of unfavorable conditions (Hollowed et al., 2001).

Adults

The distribution of the migrating coastal stock varies from about lat. 25°N to lat. 55°N, as the animals move north in summer and south in winter. Juvenile Pacific hake begin this annual feeding migration as they grow, and the northern extent of their migration increases with age, which is most likely related to fish length and swimming capability (Smith et al., 1990). Adults (i.e. fish age 3 and older, susceptible to exploitation) migrate from southern spawning areas to feed off Oregon, Washington, and British Columbia (approximately lat. 35°N to lat. 55°N) from April–May through September–October (Alverson and Larkins, 1969; Bailey et al., 1982; Francis, 1983; Stauffer, 1985; Dorn, 1995). Dorn (1997) applied geostatistical techniques to summer Pacific hake survey data for 1992 and 1995, estimat-

ing that the characteristic spatial scale of variability of these aggregations was between 20 and 30 km. Their cross-shelf distribution extends from the inner shelf out to waters more than 2,000 m deep, perhaps 40 km or more beyond the shelf break (Dorn, 1995).

North–South Distribution

Age structure, size distribution, and environmental conditions are all important factors determining the spatial distribution and annual coastwide migration of the Pacific hake stock and the availability of the fish to both monitoring surveys and commercial fishing operations. Usually the oldest, largest fish travel the greatest distances north into Canadian waters (Stauffer, 1985; Dorn, 1992) because they can apparently sustain higher swimming speeds (Ware, 1978; Francis, 1983). These fish also tend to be female in greater proportion, in part because females are on average larger than males (Dark, 1975; Beamish and McFarlane, 1985; Dorn, 1992). In addition, during warm years Pacific hake generally migrate further northward than in cool years (Dorn, 1995; Saunders and McFarlane, 1997; Wilson et al., 2000). Several key studies examining the interplay between these factors are discussed below.

Smith et al. (1990) studied the relationship between growth, fishing, oceanographic conditions, and length-at-age of Pacific hake found off Vancouver Island between 1976 and 1989. The Pacific hake samples they used in their analysis came from research and commercial trawl catches, and oceanographic data included time series of sea level height and sea surface temperature and salinity from Amphitrite Point (lat. 48°55′N, long. 125°32′W) and Tofino (lat. 49°09′N, long. 125°52.5′W). Growth and size-selective fishing pressure had the largest effect on mean length-at-age in their model, but they showed that oceanographic conditions also appeared to have a weak but significant influence. During warm years (higher sea level height, warmer surface temperatures, lower salinity, stronger poleward flow) Pacific hake were smaller on average than during cool years

(lower sea level height, cooler surface temperature, higher salinity, stronger equatorward flow). They attributed this difference to the effect of prevailing current patterns on Pacific hake migration under these different conditions. For instance, warm years were characterized by stronger poleward (or at least weaker than normal equatorward) flow, allowing smaller Pacific hake to migrate further northward into Canadian waters. By contrast, cooler years with stronger equatorward flow would allow only the larger, stronger Pacific hake to migrate further north.

Ware and McFarlane (1995) showed that warmer years (determined from sea surface temperatures measured at Amphitrite Point) were characterized by an increase in Pacific hake biomass in Canadian waters near La Pérouse Bank, an area just north of the Canada–U.S. border. Their analysis also showed an overlap in space and time between Pacific hake and euphausiid distributions around La Pérouse Bank, and they concluded that in warmer years Pacific hake deplete local euphausiid prey resources more quickly and move northward earlier than in cooler years, thus increasing predation pressure upon Pacific herring, *Clupea harengus pallasi*, stocks. Robinson and Ware (1999) used the simple regression between temperature and Pacific hake biomass that Ware and McFarlane developed to help parameterize a one-dimensional trophic model of the pelagic ecosystem in the La Pérouse Bank region, in which inter-annual variability in predator-prey relationships between Pacific hake, herring, and euphausiids were important.

In perhaps the most careful and complete study to date of environmental influences on Pacific hake annual migration, Dorn (1995) examined the relationship between monthly mean water temperatures along the west coast and the proportion of a given age class migrating into Canadian waters between 1977 and 1992. As earlier authors had proposed, Dorn (1995) also suggested that intensified northward currents and changes in prey distribution during warm years and El Niño events were likely mechanisms for increased north-

ward movement of the stock. Further, he showed that subsurface temperature anomalies were more closely correlated to Pacific hake migration than surface temperatures, and that temperatures in the "south" (lat. 30°N to lat. 42°N), where the Pacific hake begin their northward migration, were more important than the temperatures in the "north" (lat. 42°N to lat. 54°N), the feeding grounds. The southern temperature anomaly at 100 m during March–April explained the majority of inter-annual variation in the summertime abundance of Pacific hake in Canadian waters, and Dorn used this correlation to hindcast abundance for years between triennial surveys. The age structure of this stock was also important in his analysis, perhaps independent of environmental factors: older fish migrated further north than younger fish, the difference in mean distance migrated decreased between older age classes, and older age groups had a wider north–south distribution than younger age groups. Thus a change in age structure of the population, due to factors such as fishing pressure or patterns in recruitment, could alter the north–south distribution of the stock independent of, or in addition to, changes in climate-ocean conditions in the CCLME.

Although the empirical relationships reported by Dorn (1995) and Ware and McFarlane (1995) correctly capture the impact of temperature on the north–south distribution of Pacific hake, they do not conclusively establish the mechanisms by which water temperature influences Pacific hake population dynamics. Two possible mechanisms—current advection and active swimming in response to environmental cues—are thought to directly affect the summer distribution of adult Pacific hake (Smith et al., 1990; Dorn, 1995). The distribution that results from these mechanisms is affected by prevailing ocean conditions in the CCLME. The northward feeding migration begins during the winter, when poleward transport dominates. These conditions favor the northward movement of Pacific hake, and, all other factors being equal, larger and faster swimming fish will travel further north

in a given period of time. The onset of equatorward transport in surface waters and upwelling conditions after the spring transition could retard the northward movement of Pacific hake for the following reasons: they must swim against strong southward currents, they may be avoiding the coldest temperatures associated with upwelling of waters from below the thermocline, or they may find favorable feeding areas further south because the upwelling has supported high food productivity.

The beginning of the spring transition and the lag between this transition and the development of persistent upwelling are important influences on the distribution and abundance of Pacific hake in northern waters during the summer. Benson et al. (2002) reported an inverse relationship between acoustic survey estimates of Pacific hake biomass in Canadian waters from 1977 through 1998 and average upwelling anomaly over the preceding April, May, and June at 33°N, with the upwelling anomaly variable accounting for 77% of the variance in the Canadian biomass estimates. They contended that euphausiid prey availability driven by changes in ocean conditions, as well as the effect of prevailing currents on northward movement, were responsible. Emmett et al. (2006) linked the earlier appearance and increased abundance of Pacific hake off the Columbia River near the Oregon–Washington border to warm years with a late spring transition.

The evidence supporting the role of ocean conditions in the timing of the southward migration in fall is less compelling because there are fewer observations of these movements. In their review, Bailey et al. (1982) reported that Soviet fishery researchers had proposed a link between the winter appearance of the Davidson Current and the beginning of the southward migration. Thomson et al. (1989) noted that Pacific hake typically disappear from the La Pérouse area around the time of the fall transition and linked this disappearance to marked declines in production resulting from changes in oceanographic conditions associated with the fall transition. Based on observations of latitudinal clines in the biological characteristics of spawning aggregations sampled in 1991, Saunders and McFarlane (1997) suggested that the southward migration of Pacific hake might be affected by mechanisms analogous to those influencing the northern displacement.

Pockets of resident Pacific hake, whose biomass is small relative to the migratory stock, have been reported in several inlets along the west coast of Vancouver Island (Beamish and McFarlane, 1985; Ware and McFarlane, 1995). Few data and little information are available because these small resident stocks inhabit areas not subject to established or even synoptic stock assessment surveys. These Pacific hake, though considered part of the coastal (not the Strait of Georgia) stock, are in this region year round and inhabit the large sounds during the summer. Pacific hake sampled in Barkley Sound in January 1983 were juvenile fish age 1 and 2 with fork lengths of 10–15 cm and 20–30 cm, respectively (Beamish and McFarlane, 1985). Small juvenile Pacific hake (< 30 cm) usually do not migrate north into Canadian waters during the summer, much less during the winter (Stauffer, 1985; Dorn, 1992), supporting the conclusion that the fish in Barkley Sound are part of a resident local spawning stock (Beamish and McFarlane, 1985). Possibly, these populations evolved because some individuals of the migratory stock did not migrate south to spawn because of warm ocean conditions and a delay in the fall transition.

McFarlane et al. (2000) and Benson et al. (2002) in fact contended that, since the mid 1990's, increasing numbers of Pacific hake from the coastal stock have remained off the west coast of Vancouver Island year-round and have successfully spawned, due to recent climate changes. Direct evidence of spawning individuals and spawning success in these areas are lacking at present, but more recent winter observations of adult Pacific hake as far north as Nootka Sound, Vancouver Island, by Saunders et al.[5] are also consistent with this view (Fig. 6). Though most of the reproductively mature fish Saunders et al. observed were located off southern California, they also detected smaller numbers of both reproductively mature and immature Pacific hake throughout the surveyed area off the U.S. and Canadian west coasts.

There have been similar observations of adult Pacific hake present year-round in southeast Alaska.[7] In 1999, substantial numbers of these fish appeared in a year-round time series of Steller sea lion (*Eumetopias jubatus*) scat in the Frederick Sound area, near the Brothers Islands (~ lat. 57°17'N, long. 133°50'W). Between the inception of the time series in 1993 and 1999, only incidental and sporadic instances of Pacific hake had previously been observed. Midwater trawling conducted as part of ongoing studies of sea lion foraging documented midwater schools of adult Pacific hake in Frederick Sound, year-round during 2001–2004. These Pacific hake appeared to have remained well north of their traditional habitat after moving there following a strong El Niño event in 1997–98, though the northward movement of hake may have begun after a putative regime shift to warmer conditions in 1989 (Benson et al., 2002; footnote 7).

Changes in adult Pacific hake migration and distribution may in turn affect where and how well the embryos, larvae, and juveniles of succeeding year classes grow and survive. Bailey (1980) described a northward shift of Pacific hake spawning location between the mid 1960's and 1979, which he linked primarily to fishing pressure on older, larger individuals. Horne and Smith (1997) argued that the spawning locations of Pacific hake shifted north in warmer years and had moved 444 km toward the north between 1951 and 1984, based on modeling using CALCOFI collections of larval hake. They used temperatures >10°C at 100 m depth off Point Conception to define "warm years," noting an anecdotal example of an instance where surface

temperature was cool, but temperature at 100 m was one of the warmest on record at that location. While both age structure and ocean conditions are dominant factors in determining the location of Pacific hake spawning in a particular year, we suggest that the Horne and Smith study also fits more recent implications of a continued climate-mediated northward shift in the spawning location (Hollowed, 1992; Saunders and McFarlane, 1997;

Figure 6.— Circles indicate the locations of 20 midwater trawls that captured Pacific hake during a winter survey off the west coasts of Canada and the United States, 10 Jan. – 6 Feb. 2001. These trawls were not used to estimate hake abundance; they were conducted to verify acoustically detected aggregations of Pacific hake. Dots indicate those trawls that captured reproductively mature Pacific hake whose maturity stage indicated they were either in preparation for spawning or had recently spawned. The 200 m depth contour (in gray) defines the continental shelf break. Data from Saunders et al. text footnote 5.

McFarlane et al., 2000; Benson et al., 2002). These observations are at odds with the classical model of the annual Pacific hake life cycle as usually articulated (e.g. Alverson and Larkins, 1969; Bailey et al., 1982).

Cross-shelf Distribution

Pacific hake form dense daytime aggregations in regions of steeply sloping bathymetry along the shelf-break and near the edges of mid-shelf banks and basins, sometimes extending well offshore (Bailey et al., 1982; Dorn, 1995; Ware and McFarlane, 1995; Mackas et al., 1997; Swartman, 2001). Pacific hake are found primarily between 50 and 500 m below the surface during the day, most commonly in aggregations between 150 and 250 m.

Pacific hake inhabit a three-dimensional environment where their response to temperature gradients may be an important mechanism driving their depth distribution since, unlike euphausiids, Pacific hake are sufficiently strong swimmers to overcome physical mechanisms related to flow-field structures. Swartzman (1997) found that the horizontal spatial pattern of Pacific hake along acoustics-trawl survey transects perpendicular to shore was related to temperature at the depth of the fish school, bottom depth, and latitude south of Cape Flattery in 1992. The depth of Pacific hake aggregations increased moving north from lat. 42° to lat. 46°N and moving out along the continental shelf to the shelf-break. This pattern probably reflects the latitudinal clines associated with the northern migration and ontogenetic effects on depth preferences: smaller, younger juvenile fish do not migrate as far north as older Pacific hake (Hollowed, 1992; Dorn, 1995; Ware and McFarlane, 1995; Horne and Smith, 1997), and juvenile Pacific hake exhibit a preference for shallower shelf locations than mature fish, which are generally most abundant near the shelf-break (Methot and Dorn, 1995; Saunders and McFarlane, 1997).

Swartzman's (1997) analysis did not explicitly account for age and size structure of the stock, however. Both the biomass of Pacific hake in aggregations

and the number of smaller clusters forming an aggregation were significantly affected by water temperature, bottom depth, and the depth below the surface. Clusters were larger and had more biomass in the north than in the south, and maximum biomass was observed in aggregations occupying temperatures around 7°C, although Pacific hake also occupied waters with temperatures ranging from 5° to 9°C. Swartzman noted that temperature and depth were closely correlated, making it hard to separate their effects.

There are no experimental observations in the literature to establish preferred temperature ranges for Pacific hake. In the field, acoustic surveys of Pacific hake collect temperature measurements during midwater trawls and conduct a limited number of conductivity-temperature-depth (CTD) profiles. Although the midwater trawls are conducted to verify acoustic observations and are not random samples or of standard duration, they do indicate the temperatures at the depths and locations where hake were observed and captured. In the 2003 and 2005 acoustics-trawl surveys, the distribution of temperatures from trawls in which more than 50 hake were caught ranged from 5° to 11°C, averaging 6.98°C (SD 0.89) (Fig. 7, top; Fleischer et al., 2005). This is similar to the findings of Swartzman (1997) and those of prior acoustics-trawl surveys (Wilson and Guttormsen, 1997; Wilson et al., 2000; Guttormsen et al.[8]). However, in 2003 and 2005 these water temperatures were not significantly different from those hauls in which less than 50 hake (an incidental catch size) were captured (two-sample T-test, t= 0.90, df= 159, p= 0.37), and in fact these temperatures were typical of much of the water column that was sampled (Fig. 7, middle and bottom). Temperatures from hauls in which less than 50 hake were caught averaged 6.82°C (SD 1.13), and the average median profile temperature from CTD profiles was 7.56°C (SD 1.12).

Pacific hake are obviously able to live within a range of temperatures, as their distribution during anomalous years shows. For example, Agostini (2005)
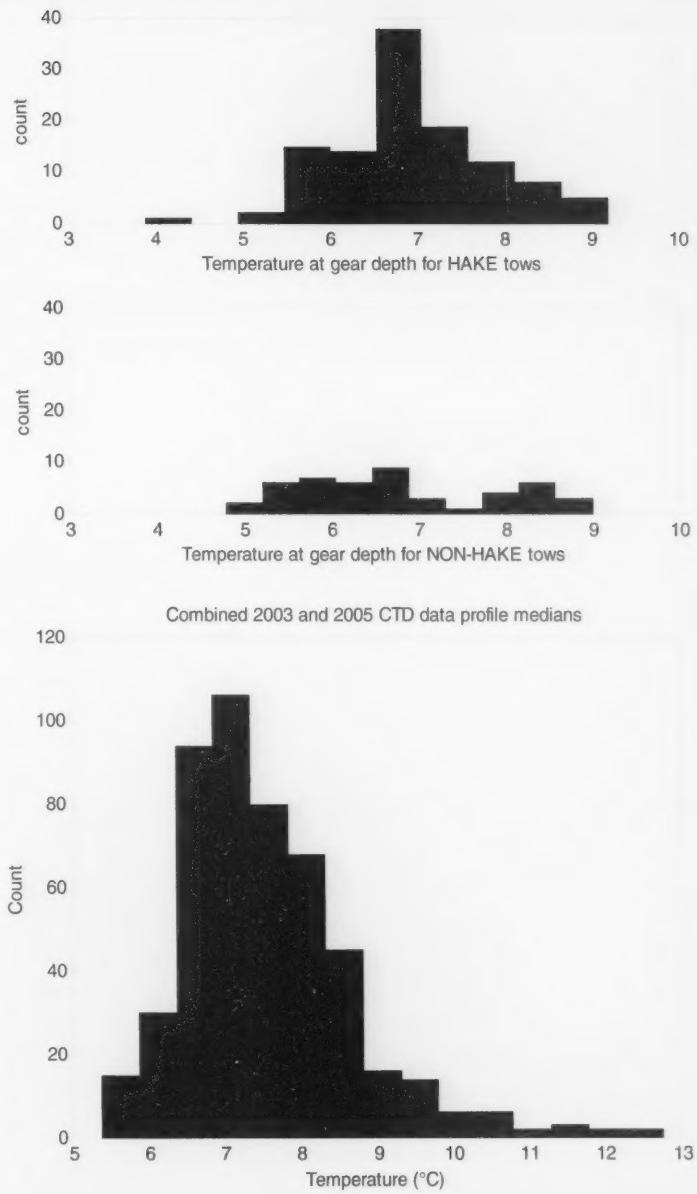
Figure 7.—Top, temperatures from sensors located on the headrope of midwater and bottom trawls that captured more than 50 Pacific hake during the 2003 and 2005 acoustics-trawl surveys of Pacific hake. Middle, temperatures from sensors located on the headrope of midwater and bottom trawls from the same surveys that captured less than 50 Pacific hake. Bottom, median temperatures from CTD profiles from the same surveys.

[8]Guttormsen, M. A., C. D. Wilson, K. Cooke, M. W. Saunders, D. R. McKelvey, and R. Kieser. 2003. Echo integration-trawl survey of Pacific hake, *Merluccius productus*, off the Pacific coast of the United States and Canada during June–August 2001. AFSC Processed Report 2003-12, Alaska Fisheries Science Center, NMFS, NOAA, US Department of Commerce, Seattle, WA, 81 p.

and Agostini et al. (2006) used hake survey biomass, CTD data from summer 1998 (when ocean conditions were very warm on the west coast at the end of an El Niño event) to show that hake were observed in much warmer waters on average (mean 12.2°C, SD 3.5) than in 1995 (mean 5.3°C, SD 2.6). Note that average temperatures from midwater trawls reflect the narrow depth range of a targeted hake aggregation, while Agostini (2005) and Agostini et al. (2006) related hake found throughout the water column to averages of temperatures from nearby CTD profiles.

We infer that there are other important determinants of the vertical distribution of Pacific hake, since temperature and depth are correlated with other factors, including currents and prey availability. Pacific hake are often found in close spatial proximity to aggregations of euphausiids (Mackas et al., 1997; Swartzman, 1997; Swartzman, 2001; Swartzman and Hickey, 2003), an important Pacific hake prey during the summer (Livingston, 1983; Livingston and Bailey, 1985; Tanasichuk et al., 1991; Ware and McFarlane, 1995; Buckley and Livingston, 1997). The relationship between euphausiids and Pacific hake may be strongest for smaller fish, since Pacific hake become increasingly piscivorous with age (Livingston, 1983; Livingston and Bailey, 1985; Tanasichuk et al., 1991). The mechanisms driving the spatial aggregation patterns of euphausiids and Pacific hake need not be the same for each of these organisms to produce the observed similarities in distribution patterns of each species. The available evidence supports the hypothesis that two mechanisms directly affect the cross-shelf distribution of Pacific hake on their feeding grounds during the summer and may be responsible for the strong overlap and spatial proximity of euphausiids and Pacific hake (Mackas et al., 1997; Swartzman, 2001): oceanographic conditions, including flow-field dynamics and predator-prey dynamics.

Bailey et al. (1982) noted that Pacific hake make a progressive movement from onshore to offshore from early to late in the summer feeding season; he speculated that this movement was related to the seasonal dynamics of the California Undercurrent. However, Tanasichuk et al. (1991) and Tanasichuk (1999, 2002) contended that predator-prey dynamics have a dominant role when Pacific hake first arrive at feeding areas on the shelf off Vancouver Island, resulting in an inshore distribution early in the summer because the higher temperatures of these shallower waters support higher productivity.

Mackas et al. (1997) held that the decline in euphausiid abundance off the west coast of Vancouver Island later in late summer, and the development of upwelling-driven high productivity offshore, led to a shift in Pacific hake distribution towards the shelf-break, where flow-field dynamics became more important influences on Pacific hake distribution. In that study, late summer distributions of Pacific hake on La Pérouse Bank occured in a band 5–10 km wide at the shelf-break coinciding with upwelling and subsequent doming of density surfaces. Based on vertical and horizontal offsets between the distributions of Pacific hake and euphausiids, Mackas et al. (1997) concluded that both Pacific hake and euphausiids were independently orienting to environmental gradients produced by turbulence associated with vertical and horizontal current shears at the shelf-break.

In a study of much broader spatial scope, Swartzman (2001) found that the spatial proximity of euphausiids and Pacific hake was dominated by overlap at or near the shelf-break based on acoustic data from the 1995 and 1998 Pacific hake acoustics-trawl surveys; Swartzman and Hickey (2003) report similar results in an analysis of data from 1995, 1998, and 2001. High abundance Pacific hake schools were often close to high abundance euphausiid patches when these aggregations were close to the shelf-break, but this pattern of overlap was far less obvious along portions of transects further offshore. Swartzman (2001) suggests a simple causal sequence in which euphausiids sense and orient to oceanographic factors (bottom depth, temperature, flow) and Pacific hake sense and orient to euphausiids to explain the aggregation patterns that he

observed. Several recent studies have linked the distribution of euphausiid aggregations off the west coast to the California Undercurrent (Swartzman et al., 2005) and mesoscale physical processes in the CCLME (Ressler et al., 2005; Pierce et al.[9]).

Diel and Seasonal Migrations

In addition to their seasonal, coast-wide migration, adult Pacific hake also migrate on shorter time scales during most of the year. They form well-defined pelagic schools during the day, mostly between depths of 50 and 500 m, disperse and undertake a diel vertical migration toward the surface at dusk, and then migrate back to mid-water depths during the daytime, except during spawning, when they neither feed nor migrate vertically (Best, 1963; Alverson and Larkins, 1969; Nelson and Larkins, 1970; Bailey et al., 1982; Stauffer, 1985). The vertical migration is usually thought to facilitate predation upon fish and zooplankton in the water column (Alton and Nelson, 1970), but few careful and complete studies of diel Pacific hake feeding behavior have been done.

Livingston (1983) showed that stomach fullness was irregular in samples collected over a 24 hour period, but was highest at around 1800 h, well before dusk in mid summer. Tanasichuk et al. (1991) contended that Pacific hake in his study fed periodically during the daytime throughout the feeding season. The Livingston (1983) and Tanasichuk et al. (1991) studies suggest significant feeding bouts during daytime, after midnight, and in the early morning, in contrast to previous reports of primarily nighttime feeding (Alton and Nelson, 1970; Rexstad and Pikitch, 1986). However, these conclusions of preferential nighttime feeding by Pacific hake were inferred from daytime stomach fullness data and Pacific hake diel behavior, while Livingston (1983) and Tanasichuk et al. (1991) collected Pacific hake stom-

[9]Pierce, S. D., J. A. Barth, W. T. Peterson, and T. J. Cowles. Bioacoustical analysis of zooplankton distributions during mesoscale surveys in the Northern California Current System. Deep-Sea Res. I. Manuscript in prep.

achs during both night and day in their studies. Still, Krutzikowsky and Emmett (2005) recently compared daytime and nighttime catches of pelagic surface trawls, in which Pacific hake appeared only at night, and reported that stomach contents of those fish suggested active nighttime feeding. It may be that feeding by Pacific hake occurs during both night and day, depending on prey availability (Emmett et al., 2006), and that Pacific hake migrate vertically both to seek prey and also to avoid other visual predators in surface waters during the daytime.

This sort of tradeoff between risk and reward for vertical migration is well discussed for both zooplankton and fish in the literature (Angel, 1985; Neilson and Perry, 1990; De Robertis, 2002). Vertical migration could also have bioenergetic advantages for Pacific hake if the growth efficiency of the animal is greater at lower temperatures in deeper water (e.g. 7° to 8°C for Pacific hake), but feeding rates and feeding efficiency are greater at higher temperatures near the surface. In this scenario, it would be advantageous for hake to feed at the higher temperatures for a short time and digest, assimilate, and grow at the lower temperatures. As with other marine fishes, diel migration may be a facultative behavior (Neilson and Perry, 1990) for Pacific hake, influenced by several important factors (prey, light, avoidance of predation, metabolism) and sensitive to local environmental conditions.

Prey and Predation

Larvae and smaller juvenile hake feed on copepod eggs, copepods, and juvenile euphausiids (Sumida and Moser, 1980; Grover et al., 2002; Cass-Calay, 2003). The diet of large juveniles and adults is composed largely of euphausiids, fish, and pandalid shrimp, with evidence of adult cannibalism on juveniles (Alton and Nelson, 1970; Bailey et al., 1982; Livingston, 1983; Livingston and Bailey, 1985; Rexstad and Pikitch, 1986; Brodeur et al., 1987; Tanasichuk et al., 1991; Buckley and Livingston, 1997; Buckley et al., 1999; Tanasichuk, 1999; Romaine et al., 2002; Tanasichuk, 2002). The amount of cannibalism of adults upon juveniles (intra-cohort can-

nibalism is not common) is probably related to the amount of spatial overlap between juvenile and adult fish, which could vary annually as the distribution of the hake stock changes (Buckley and Livingston, 1997). The daily ration for juvenile and adult Pacific hake has been estimated variously between 0.4 and 3.5% of body weight per day in the literature (Francis, 1983; Livingston, 1983; Rexstad and Pikitch, 1986; Tanasichuk et al., 1991).

Pacific hake is probably the most important consumer of zooplankton and forage fish in the CCLME (Field, 2004). Larger zooplankton and fish become more important dietary components as Pacific hake grow larger, implying a strong interaction between size and the prey that the Pacific hake are able to capture, but the availability of suitable prey in the environment and the spatial and temporal overlap between the predator and these prey are probably equally important (Livingston and Bailey, 1985). Larger fish most likely have more flexibility in prey size and type. Pacific hake appear to be opportunistic feeders (Best, 1963), particularly upon schooling or aggregating prey (Livingston and Bailey, 1985), and anecdotal evidence suggests they can be voracious predators on whatever becomes available (e.g. Hobson and Howard, 1989).

Euphausiids nearly always appear as a very important component of Pacific hake diet, but some studies, reviewed by Bailey et al. (1982) and Livingston (1983) have demonstrated seasonal patterns in the mix of prey types utilized throughout the CCLME. Observed dietary shifts have been from primarily euphausiid prey to increased consumption of Pacific herring in late summer off Vancouver Island (Tanasichuk et al., 1991; Ware and McFarlane, 1995), and from mostly fish prey to euphausiids in the summertime off Oregon and Washington (Brodeur et al., 1987).

Interrannual variation in Pacific hake diet has also been reported, including changes in the proportion of euphausiids and fish eaten and the species present (Livingston, 1983; Brodeur et al., 1987; Buckley and Livingston, 1997). Tanasichuk (2002) reported that Pacific hake

daily ration varied significantly among years during 1985–98 in August off Vancouver Island, but the proportion of the daily ration composed of euphausiids (mostly *Thysanoessa spinifera* >17 mm in length) averaged 89% even as euphausiid prey became less abundant. Nelson (2004) reported that consumption of euphausiids by Pacific hake was reduced during the 1997–98 El Niño, supplanted in the diet by Pacific herring in the larger, more piscivorous fish (> 50 cm in length); he attributed this change to an interannual shift in the availability of euphausiids and Pacific herring. Smaller Pacific hake that were not able to consume herring suffered a reduction in diet quality and perhaps growth. Similarly, some authors reported that Pacific hake growth was depressed during the 1983–84 El Niño (Hollowed and Francis, 1987; Francis et al.[10]), perhaps due to reduced euphausiid abundance (Miller et al., 1985; Rexstad and Pikitch, 1986). Pacific hake appear to respond to changes in climate-ocean conditions and prey fields, but moving from descriptive observations to predictive relationships between Pacific hake, the variability in prey species (such as euphausiids and herring) abundance, and oceanographic conditions at different scales has been difficult (Hayward, 2000; Mackas et al., 2001; Benson et al., 2002; Tanasichuk, 2002; Field et al., 2006b).

In addition to being a significant predatory force in the CCLME, Pacific hake are also important prey for other species. During early ontogeny, Pacific hake embryos and larvae are preyed upon by copepods, amphipods, and gelatinous zooplankton (Bailey and Yen, 1983; Livingston and Bailey, 1985). Pacific hake juveniles and adults are also prey for other nekton, including dogfish, *Squalus acanthias;* sablefish, *Anoplopoma fimbria;* lingcod, *Ophidon elongates;* arrowtooth flounder, *Atheresthes stomias;* rockfishes, *Sebastes*

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[10]Francis, R. C., G. A. McFarlane, A. B. Hollowed, G. L. Swartzman, and W. M. Getz. 1984. Status and management of the Pacific hake (*Merluccius productus*) resource and fishery off the west coast of the United States and Canada. Northwest and Alaska Fisheries Center Processed Report NWAFC-84-18, 73 p.

spp.; tunas, *Thunnus* spp. (Fiscus, 1979; Livingston and Bailey, 1985); as well as apex predators such as marine mammals (reviewed by Fiscus, 1979; Ainley et al., 1982; and Baraff and Loughlin, 2000) and seabirds (Livingston and Bailey, 1985; Field, 2004). The predation of Humboldt squid (*Dosidicus gigas*) upon adult Pacific hake has recently received attention (Zeidberg and Robison, 2007; Field et al., 2007) as these squid have become more common in the northern CCLME. Thus, Pacific hake form an important link between upper and lower trophic levels.

Pacific hake is the most abundant groundfish off the North American west coast, south of Alaska (Methot and Dorn, 1995), and its biomass—the largest of any single groundfish species in the CCLME—supports a substantial fishery and exerts a wide influence as both predator and prey (Field, 2004). Changes in the migration and distribution of Pacific hake could alter its predatory impact upon populations ranging from ocean shrimp, *Pandalus jordani* (Hannah, 1995), and euphausiids to forage fishes, juvenile salmon, *Oncorhynchus* spp. (Emmett, 2006), and younger age classes of Pacific hake (Buckley and Livingston, 1997), as well as alter its availability as prey to marine mammals (Ainley et al., 1982) and seabirds (Livingston and Bailey, 1985). Francis (2003) proclaimed Pacific hake the "poster child of the California Current", emphasizing that this fish "[serves] as a massive stabilizing bridge between the northern and southern parts of the California Current ecosystem" and is distributed "in response to physical and biological cues which vary greatly from year to year." The distribution, abundance, and behavior of coastal Pacific hake is sensitive to climate-ocean conditions, making it a useful biological indicator of changes in the CCLME (Benson et al., 2002).

Fishery, Management, and Monitoring

A Brief History of the Fishery

Methot and Dorn (1995) and Sylvia (1995) reviewed the history of the fishery and market for Pacific hake. During the 1960's, the fishery for Pacific hake in the United States initially developed as a tiny domestic fishery, with annual landings of only hundreds to a few thousand tons. Beginning in 1966, the fishery was dominated by a much larger, mostly foreign effort, with annual landings averaging 137,000 t. The foreign fishery was in turn eclipsed by a joint-venture fishery in the early 1980's. An exclusively domestic fishery was eventually established in 1991, with offshore factory and catcher vessels, vessels delivering to shoreside processing plants, and tribal fisheries splitting the U.S. allocation. The development of the Pacific hake fishery in Canadian waters was largely similar (Beamish and McFarlane, 1985; Helser et al., 2006), becoming a mostly domestic, shoreside fishery by 2001 and now allocated using individual vessel quotas.

The early stages of the fishery produced mainly fillets, headed and gutted products, and fish meal, mostly for foreign markets. Initially, there was very little market in either the United States or Canada for the catch, due to problems with rapid softening of the flesh related to the presence of the parasites in the genus *Kudoa* (Kabata and Whitaker, 1981, 1985, 1986). By the early 1990's, quality problems were overcome by rapid cooling techniques and enzyme inhibitors, and the development of processed Pacific hake products, such as surimi, has made the fishery more profitable (Methot and Dorn, 1995).

Like other fisheries on the west coast, the Pacific hake fishery is monitored by observers. Currently, observers are mainly concerned with monitoring total catch and accounting for bycatch of other fish stocks (which constitutes a small fraction of the total Pacific hake catch, but can be relatively significant for very depleted stocks). They also collect biological samples for stock assessment-related scientific work. Deployment of U.S. fishery observers to monitor the catch on foreign vessels in the Pacific hake fishery began in 1977, more than two decades before most other U.S. west coast fisheries carried observers. Domestic factory and catcher

vessels in the Pacific hake fishery voluntarily began carrying observers in 1991, in what was essentially an outgrowth of the observing conducted on many of these same vessels in the Alaska walleye pollock, *Theragra chalcogramma*, fishery. Vessels delivering Pacific hake to shoreside plants at first operated under experimental fishing permits and did not carry observers, but complete observer coverage in the U.S. Pacific hake fishery is now mandatory, with human observers monitoring offshore factory and catcher vessels, and cameras and port samplers monitoring the catch of vessels delivering to shoreside plants (Tuttle[11]) In Canada, fishery observers were first deployed on foreign vessels targeting Pacific hake in 1987. Since 1996, on-board observers have monitored and sampled the catch of all domestic groundfish vessels, and all landed catch from trawlers is subject to dockside monitoring (McFarlane, 2001).

Management Strategy and Challenges

Pacific hake are caught commercially by mostly midwater trawling during April–November in offshore waters along the coasts of northern California, Oregon, Washington, and British Columbia (Helser et al., 2006). A quota is set annually, and fish are harvested by both Canadian and U.S. fishing fleets. In past years, landings have exceeded the international coast-wide total allowable catch (by an average of 14% between 1991 and 1999) due to disagreements on the allocation between Canadian and U.S fisheries, but since 2000 the coastwide catch has been maintained within the quota (Helser et al., 2006).

In November 2003, Canada and the United States signed a new binational treaty for the joint management of Pacific hake to establish a process under which the total allowable catch (TAC) is decided and the fishery is managed. Under the new agreement, 26.12% of the TAC will be allocated to Canada and 73.88% will be allocated to the United

States. The terms of the treaty have not yet been fully implemented by either nation, but the most recent stock assessments and management activities have conformed to the spirit therein (Helser et al., 2006).

Utilization of the TAC is limited not only by the status of the Pacific hake stock, but also the bycatch of other species in the Pacific hake fishery. While this bycatch represents a relatively small fraction of the annual landings in the Pacific hake fishery, it is large enough to exceed limits on other severely depressed West Coast groundfish stocks, including several species of rockfish (*Sebastes* spp.) (Helser et al., 2006; He et al.[12]).

As noted, the Pacific hake stock is characterized by low recruitment punctuated by very strong year classes, so the fishery must be managed to maintain the stock until the next large year class appears. The best indicator of potential recruitment remains the monitoring of larvae and juvenile abundance, as discussed earlier. Helser and Martell (2007) describe the most recent stock assessment, including history of the time series, sources of data, and model development (see also Fig. 2). Primary data inputs to the assessment model include catch and age data from the fishery, recruitment indices from larval and juvenile surveys and the biennial (formerly triennial) joint U.S.–Canada acoustics-trawl survey of adult Pacific hake. The latter survey is the only fishery-independent measure now used to assess the adult stock.

The Acoustics-Trawl Survey: Monitoring the Recruited Pacific Hake Stock

Fishery-independent acoustic surveys to assess the distribution and abundance of the coastal stock of Pacific hake have been conducted since 1977 by NMFS, and jointly with Fisheries and Oceans Canada since 1995, based on the recog-

nition that this stock is a transboundary resource (Fleischer et al., 2005). The current survey design is based upon knowledge of the biology of the fish and the historical distribution of the stock, past survey coverage, statistical considerations, and logistical constraints. It assumes that the surveyed area encompasses the entire summer range of the recruited stock, and that most or all of the stock is available to the survey techniques at the time of the survey.

Broadly speaking, the survey measures volume backscattering strength (S_v) at 38 kHz along east–west oriented transects spaced at 18.5 km (10 n.mi.) intervals along the U.S. and Canadian west coasts (Fig. 5). Backscatter attributed to Pacific hake is integrated into units of backscatter per unit area (s_A) and then converted into an estimate of Pacific hake biomass and numbers using information from concurrent midwater and bottom trawling (Fleischer et al., 2005). These data are incorporated into the Pacific hake stock assessment model (Helser et al., 2006). Basic oceanographic information is also collected during the survey, including regular CTD profiles.

The survey takes place in the summer months (between June and September), when adult Pacific hake are found at the northern extent of their annual coastal migration along the continental shelf and slope (Alverson and Larkins, 1969; Bailey et al., 1982). Typically, the survey stretches from near Monterey, Calif. (lat. 36°30′N), to Queen Charlotte Sound, B.C. (lat. 54°30′N), extends from about 50 m of water nearshore to water depths of 1,500 m or more, and requires about 65–75 days to complete, including coverage of both U.S. and Canadian waters. The survey was a triennial effort until 2003, when a biennial schedule was implemented to increase the frequency of the stock status information required for management.

The design of Pacific hake monitoring surveys since the mid 1970's reflects the state of knowledge of adult Pacific hake distribution during the summer feeding season, since the survey is intended to capture the entire population. The survey design was changed in the early 1990's

(Dorn et al., 1994; Dorn, 1996; Wilson and Guttormsen, 1997) to increase the offshore extent (to 1,500 m water depth) and northward extent (as far as southeast Alaska, lat. 58°N) of the survey, to account for significant portions of the population in those areas during some years (Saunders and McFarlane, 1997; Fleischer et al.[13]).

It is unclear whether these changes were necessary solely because of changes in Pacific hake distributional patterns since the survey was first designed (Dark et al., 1980; Nelson and Dark, 1985), or because in later years fractions of the population that had always been "missed" by the old sampling design and gear were detected. The entire Pacific hake stock assessment time series was retrospectively adjusted using "expansion factors" for these changes in sampling design (Dorn et al., 1994; Dorn, 1996; Wilson and Guttormsen, 1997).

Major areas of uncertainty in this survey are pointed out in recent stock assessments (e.g. Helser et al., 2006) and Stock Assessment Review (STAR) Panel[14] reports. Topics identified as major contributors to the uncertainty in survey-based biomass estimates and requiring additional research include (among others) the relationship between acoustic target strength and length for Pacific hake, a key parameter for acoustics-based biomass estimates (Traynor, 1996; Fleischer et al., 2005; Henderson, 2005); improved information on life history parameters, including growth rates and maturity; and the effect of climate-ocean conditions on movement patterns (expansion/contraction) of the stock and their effect on survey selectivity and the availability of the stock to the survey technique (the catchability of the survey, or q) during different survey years.

[13]Fleischer, G. W., P. H. Ressler, R. E. Thomas, S. K. de Blois, and L. H. Hufnagle. 2005. NWFSC regional protocols for the joint Canadian and U.S. Pacific hake acoustic survey. NMFS, Northwest Fisheries Science Center (NWFSC), Fishery Resource Analysis and Monitoring Division Acoustics Team.

[14]STAR panel. 2006. Report of the joint Canadian and U.S. Pacific hake/whiting Stock Assessment Review Panel. 6–9 Feb., 2005, Seattle, WA. Online at http://www.pcouncil.org/groundfish/gfstocks.html.

[12]He, X., S. V. Ralston, A. D. Maccall, D. E. Pearson, and E. J. Dick. 2003. Status of the widow rockfish resource in 2003. Draft submitted to the June 2003 council meeting. Online at http://www.pcouncil.org/groundfish/gfsafe0803/gfsafe0803.html.

Recent research into climate-ocean patterns and processes in the CCLME and their relevance for Pacific hake recruitment, distribution, and abundance, all have direct bearing upon improved Pacific hake stock assessment.

Recent Observations of Climate-Ocean Influences on the Distribution of Pacific Hake

The influence of climate-ocean conditions on the Pacific hake has been recognized during the major reviews of the state of knowledge of the stock over the past 20 years (Bailey et al., 1982; Stauffer, 1985; Methot and Dorn, 1995). As we have noted in this review, the survival of Pacific hake larvae and juveniles are linked to processes such as upwelling and advection, thereby affecting recruitment in different years and the strength of different year classes. It is also widely recognized that the annual coast-wide migrations of adult Pacific hake change in different climate ocean conditions, a phenomenon most dramatic during anomalous years.

But the mechanisms underlying these phenomena have not been fully elucidated, and perhaps as a consequence, these observations have been slow to change the conceptual model of Pacific hake autecology and have not been fully incorporated into the stock assessments that drive management decisions. Some early Pacific hake assessments used different recruitment curves during warm v. cold conditions (Swartzman et al., 1983; Hollowed and Francis, 1987; Francis et al.[10]), but the current stock assessment construct does not explicitly use environmental covariates (Helser et al., 2006), although its modeling of selectivity may implicitly incorporate the effect of ocean conditions on Pacific hake distribution (Agostini, 2005).

However, there is an increasing trend of environmental factors being explicitly handled in stock assessment models (Schirripa and Colbert, 2006). In the 10 years since the last major review of the status of knowledge of the Pacific hake stock (Methot and Dorn, 1995), there have been several recent advances in our understanding of climate-ocean influences upon Pacific hake. In large part, the last 10 years have provided new data with which to evaluate some longstanding ideas about Pacific hake abundance and distribution.

Northward Shift in Spawning Location

It is likely that coastal Pacific hake are spawning further north now than suggested by the classic model as articulated by Alverson and Larkins (1969), Bailey et al. (1982), and by most published papers on this species, one notable exception being the review of climate influences on North Pacific fish stocks by McFarlane et al. (2000). Unusual distributions of age-0 Pacific hake (Pearcy and Schoener et al., 1987; Dorn, 1996) imply that spawning events north of California can occur during warm ocean periods, and that the traditional model of hake annual migration, originally formulated in the late 1960's, should be revised to so that it can accommodate such observations (Fig. 8).

We further hypothesize that more northerly spawning events have continued through the 1990's and into the 21st century, and that these events reflect a general sensitivity of adult Pacific hake distribution not only to anomalously warm and cool years, but also to longer-term warming in climate-ocean conditions in the CCLME (McFarlane et al., 2000; Mendelssohn et al., 2003; Palacios et al., 2004; King, 2005; Field et al., 2006a).

Assuming that the distribution of young-of-the-year fish indicates the location of offshore adult spawner concentrations, more recent reports of young-of-the-year hake off Oregon, Washington (Phillips et al., 2007), and Vancouver Island (Cooke[15]) in mid summer (Brodeur et al., 2006) are consistent with this pattern. The design of the survey presently conducted by NMFS-PWCC (Phillips et al., 2007) includes parts of the northern California, Oregon, and Washington coasts not sampled by previous larval and juvenile surveys which focused on central and

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[15]Cooke, K. 2006. Fisheries and Oceans, Canada, Pacific Biological Station, Nanaimo, BC V9T 6N7. Personal commun.

southern California (Grover et al., 2002; Fig. 5). NMFS-PWCC results show a distinct northern shift in the distribution of young-of-the-year hake, with age-0 individuals detected as far north as 47°N since 2001. Given our knowledge of how embryos and larvae disperse from spawning areas, these observations are hard to reconcile with the past convention that depicts spawning aggregations only occurring in the deep waters off the Southern California Bight.

Future research should incorporate a new conceptual model of Pacific hake annual migration, in which 1) the average spawning location can shift northward from southern California, and 2) the location of spawning is variable with groups of Pacific hake spawning in different places, well north of where the classic model would suggest during some years (Fig. 8). Studies of the variability in hake recruitment that only consider processes within the classical southern spawning area (Mullin et al., 2000) are no longer adequate.

Pacific Hake Distribution and Growth in Relation to Climate-Ocean Processes

As we have noted, studies investigating inter-annual variation in the distribution of Pacific hake in relation to ocean variability have reported a progressive increase in northern dispersal throughout the 1990's and into the 2000's. The increased northern displacement in the 1990's occurred during a period of warmer surface temperatures and reduced upwelling and stratification of coastal waters following the 1989 regime shift (King, 2005) and was related to warmer surface waters and stronger poleward flow in the spring (Ware and McFarlane, 1995; Swartzman and Hickey, 2003).

Benson et al. (2002) hypothesized that the 1989 regime shift also differentially affected the availability of euphausiids in the northern and southern regions of the CCLME, with feeding conditions in the north improved relative to those in the south, resulting in faster growth of juveniles in the northern regions during the 1990's. This progressive increase in northern distribution culminated with

Spring migration to summer distribution   **Fall migration and winter spawning**
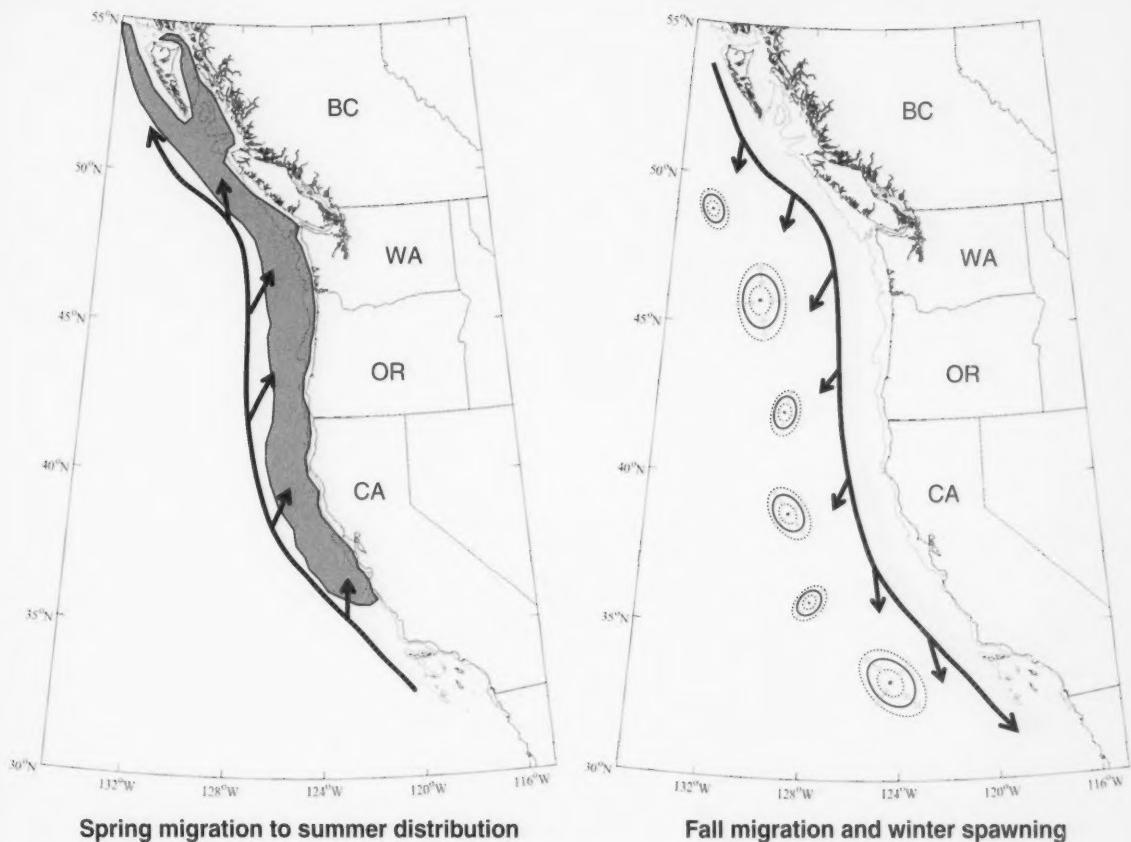
Figure 8.—Left, shaded area represents summer distribution of adults on shelf and slope in recent years. Right, ovals represent variable, patchy offshore spawning locations, inferred from recent collections of larvae and young juveniles and reports of a northward shift of spawning location in the literature. Arrows indicate the general direction of movement and migration in both panels. The 200 m isobath is shown in gray.

the cataloguing of measurable quantities of Pacific hake biomass as far north as southeast Alaska during the strong 1997–98 ENSO event (Wilson and Guttormsen, 1997; Wilson et al., 2000).

These changes in Pacific hake distribution represent a shift in the distribution of the entire stock rather than a range expansion or contraction (Benson et al., 2002), which is demonstrated by the fact that the proportion of the total Pacific hake biomass in Canadian waters increased while the proportion off southern California decreased during this period (Swartzman and Hickey, 2003), especially during the 1998 acoustic survey. The observed relationship between age, length, and northward migration distance that we have noted also implies that younger, smaller fish will increasingly appear in Canadian waters during warmer climate-ocean conditions.

Recent acoustic survey observations (Fig. 9) continue to show that the summer Pacific hake distribution includes areas north of Vancouver Island (ca. lat. 50°N) which were not considered typical Pacific hake habitat prior to the 1992 survey. Particularly dramatic are northward shifts in distribution in 1998 after a strong El Niño event, a southward shift in 2001 (Wilson et al., 2000; Guttormsen et al.[8]) after a series of cool La Niña years (Schwing et al., 2002), and subsequent movement back northward in 2003 (Fleischer et al., 2005) and 2005 (Fleischer et al.[4]) during years characterized by warmer ocean conditions and delayed upwelling in the CCLME (Brodeur et al., 2006; Pierce et al., 2006). These patterns reinforce the presence of both a relationship between shifts in north–south distribution and inter-annual physical variability, and a pattern of increasing northward dispersal during a longer-term trend of rising ocean temperatures. Such observations
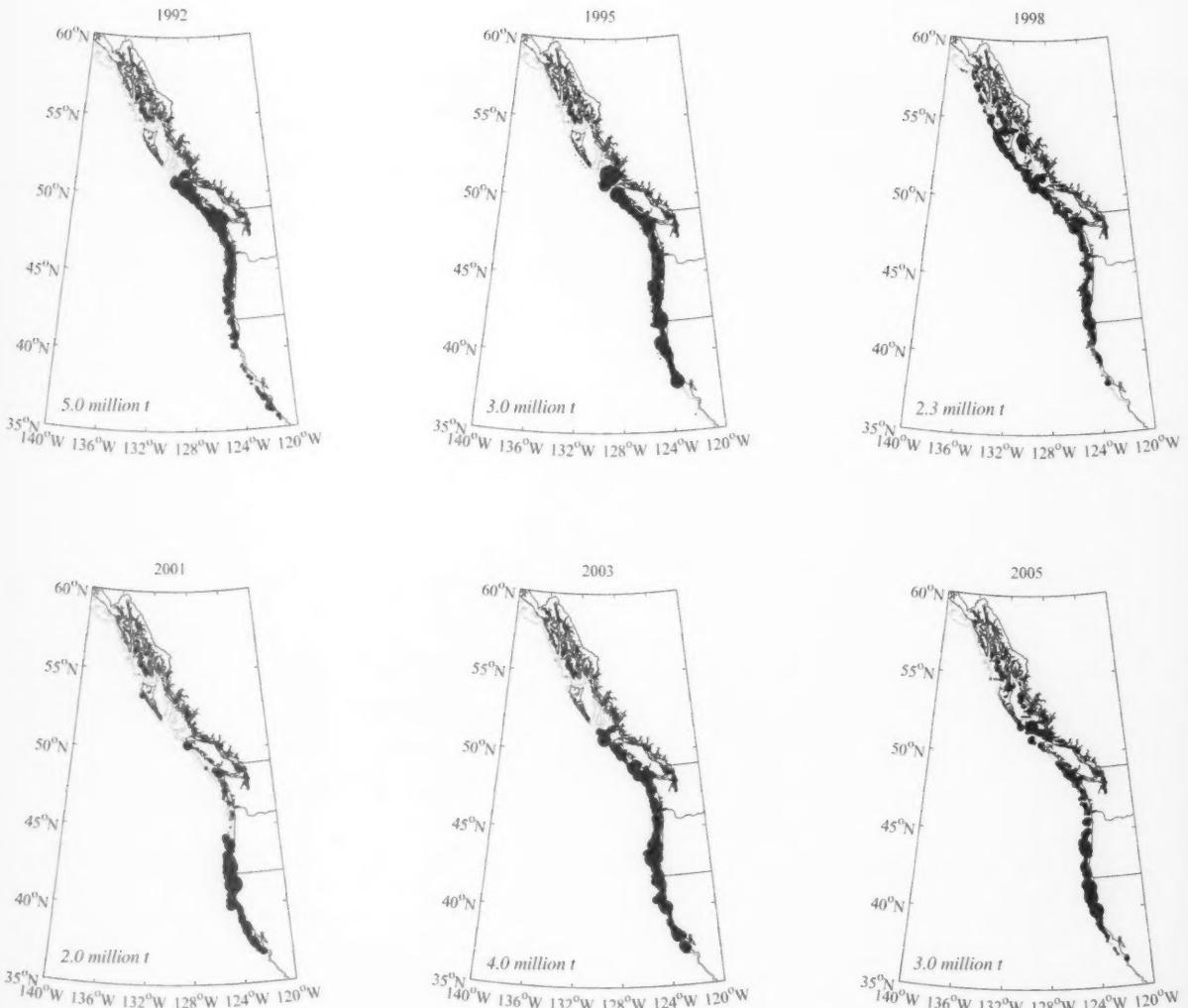
Figure 9.—The dark shaded area represents the coast-wide distribution of Pacific hake biomass during joint U.S.–Canadian acoustics-trawl surveys between 1992 and 2005. The total stock biomass from the corresponding year, estimated by the assessment model (Helser and Martell, 2007), is indicated in the lower left corner of each panel. Survey transects are indicated by solid east-west black lines, the coastline is shown in black, and the 200 m isobath is shown in gray. Between 1992 and 2001, U.S. and Canadian surveys were conducted semi-independently and their coverage overlapped in Canadian waters; for clarity, in these areas of overlap the data from Canadian surveys are not shown. Most transects have a north-south spacing of 10 n.mi., but note finer scale sampling off Vancouver Island in 1992, 1995, and 1998. For further information on these surveys, see Dorn et al. (1994), Wilson and Guttormsen (1997), Wilson et al. (2000), Fleischer et al. (2005), Fleischer et al., text footnote 4, and Guttormsen et al., text footnote 8.

not only hold promise for understanding and forecasting hake distribution, but they also imply that Pacific hake might be useful indicators of change within this ecosystem.

The proposition that ocean conditions affect Pacific hake distribution is not a new idea. The last 10 years have led to a better understanding of the strong link of Pacific hake distribution to climate-related physical processes in the CCLME (McFarlane et al., 2000; King, 2005; Field et al., 2006a), as well as the luxury of a longer time series with which to evaluate the fluctuations of the Pacific hake stock under different environmental conditions. Temperature is easily measured and has predictive power (Dorn, 1995; Ware and McFarlane, 1995), but it may not be the key variable that affects the distribution of Pacific hake, as other authors have suspected (Benson et al., 2002).

We have already discussed covariation of Pacific hake distributions with flow regimes and prey distribution: the work of Mackas et al. (1997), Swartzman (2001), Swartzman and Hickey (2003), and Benson et al. (2002) argues strongly that these are key to understanding Pacific hake distribution. Agostini (2005) and Agostini et al. (2006) recently examined and modeled the distribution of adult Pacific hake with respect to the location and intensity of the poleward undercurrent during 1995 and 1998, providing further support for this sort of link. Agostini's major finding is that Pacific hake aggregated close to the poleward flow of the California Undercurrent, perhaps in response to cues in the flow field. She showed that there was a dome-shaped relationship between Pacific hake habitat favorability and current speed, in which Pacific hake are most often found in areas of poleward flow (Fig. 10). Agostini (2005) used this relation to model the southern part of Pacific hake habitat (ca. lat. 38°–43°N), and found that there was more favorable habitat (based on a model using flow and bottom depth as predictors and accounting for autocorrelation in the data set) in 1998 than 1995 (51% vs. 16%). The model used subsurface flow between 120 and 330 m and bottom depth as
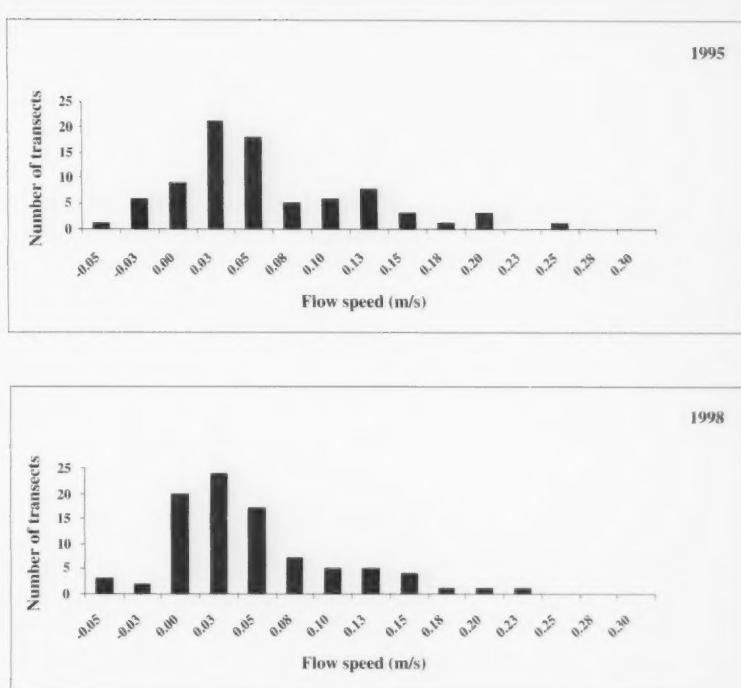
Figure 10.—Frequency distribution of alongshore flow, averaged over survey transects from depths where Pacific hake were present, based on acoustics-trawl survey data from 1995 and 1998. Positive flow speeds are poleward, characteristic of the California Undercurrent, while negative values indicate equatorward flow. Modified from Agostini (2005) with permission.

predictors, but it did not explicitly account for the possible influence of the age structure of the population.

As we have noted, climate-ocean conditions not only affect the behavior of the Pacific hake, in terms of movements and migration, but also their growth. A recent study by Colbert et al.[16] showed that oceanographic conditions could explain much of the variability in Pacific hake otolith growth increments formed between 1970 and 2002, reinforcing a link between the size of these increments and climate-ocean conditions (Dorn, 1992; MacLellan and Saunders, 1995). This link provides strong support

for a relationship between Pacific hake growth, adult distribution and migration, and climate-ocean processes.

Pacific Hake Trophic Impact and Importance

As noted, Pacific hake have a wide ranging trophic impact and importance in the CCLME. This feature has been recognized previously, but only recently have improvements in our understanding of climate-ocean processes, associated biological impacts in the CCLME, and computational improvements made realistic ecosystem-wide model simulations possible. A northward distributional shift, for example, could alter the predatory impact of Pacific hake as well as influence its availability to top predators.

Field (2004) recently formulated a mass balance model of the CCLME,

[16]Colbert, J. J., M. J. Schirripa, and O. Rodriguez. Interannual changes in Pacific hake (*Merluccius productus*) growth in relation to oceanographic conditions. Contact J. Colbert, Oregon State University, 2032 S.E. Marine Science Dr., Newport, OR 97365. Manuscript in prep.

primarily to explore the idea of eco-system-based fisheries management (Field et al., 2006b). The model includes physical forcing as well as biological data to simulate different climate-ocean conditions, and includes zooplankton, fish, and higher predators represented as single species or groups of species. Inclusion of climate indices significantly improved the fit of the model. Moreover, Pacific hake was identified by the model as a key species in the CCLME: changes in its relatively substantial abundance have wide-ranging effects, both upon forage fishes and upon the apex preda-tors that feed on Pacific hake (Fig. 11; Agostini, 2005). As a better functional understanding of climate-ocean effects emerges, such models can be used to test hypothesis and forecast future scenarios, based on assumed future environmental conditions.

Research Needs and Priorities

We suggest the following priorities for future Pacific hake monitoring and research efforts.

1) Analyze climate and Pacific hake acoustics-trawl survey data from 1992 to present to look for predic-tive relationships between Pacific hake distribution and recent cli-mate and oceanographic data. The spatial distribution of the Pacific hake stock affects its availability to both monitoring surveys and the commercial fishery. The most careful model of ocean influences on northward migration by Pacific hake, formulated by Dorn (1995), was based only on data through 1992. Modeling of distribution must include both oceanographic

factors (such as temperature, time of spring transition, climate indi-ces, and current patterns) and the age structure of the population. A predictive relationship will allow an evaluation of past survey data and improvements in the design and execution of future surveys. It will also allow better forecasts of Pacific hake distribution and ecosystem impact under different hypothetical climate-ocean scenarios.

2) Pursue improvements to the bien-nial acoustics-trawl survey, includ-ing possible adjustments to the current design based on improved understanding of relationships be-tween ocean conditions and Pacific hake distribution, as well as better knowledge of a key acoustic pa-rameter, target strength. Continue to conduct spatially expanded sur-veys of larval and juvenile stages as an index of recruitment. These research priorities closely coincide with many of the recommendations of the STAR panel convened to review the most recent stock as-sessment.[14]

3) Investigate mechanisms underly-ing observed correlations between physical oceanographic parameters and Pacific hake distribution. This will require regular collection of physical oceanographic data as well as sampling of the potential prey field which, if sufficient time and resources are allocated, could be accomplished in concert with the biennial acoustics-trawl survey. Smaller, dedicated studies of diel feeding behavior, prey consump-tion, and the available prey field that focus on the goal of establish-ing links between relevant physical variables and prey distribution are needed. These could also allow a better understanding of the mecha-nisms that drive Pacific hake abun-dance and distribution, improving monitoring and assessment of this species.

4) Develop the means for better in-formation on Pacific hake during the non summer months (after they have left the northern feeding
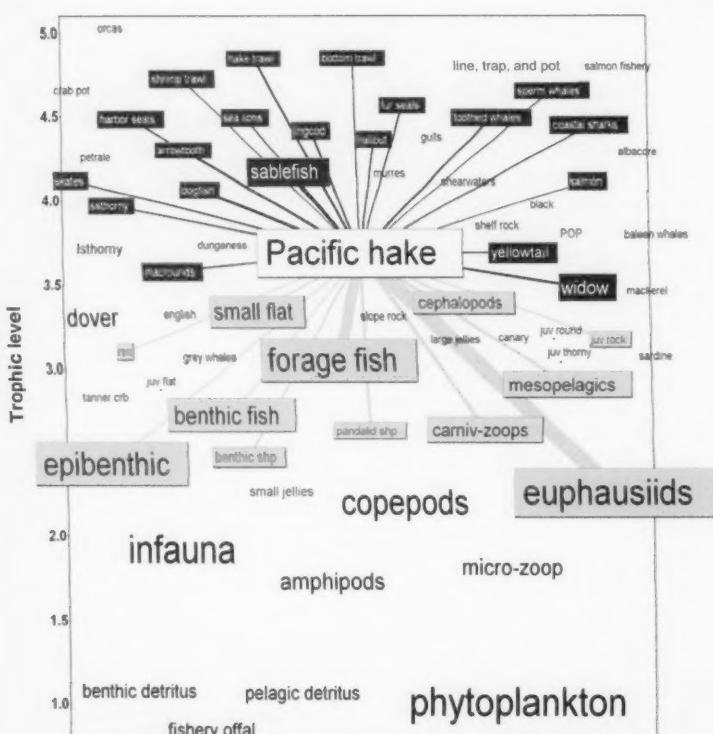
Figure 11.—The trophic position of the Pacific hake in a recent model of the CCLME. Predators on Pacific hake are shown in black boxes, prey in gray boxes, and ecosystem model components not directly connected to Pacific hake in plain text. Modified from Field (2004) with permission.

grounds) since relatively few data on Pacific hake have been collected during this time of the year. Bailey et al. (1982) noted that efforts to tag Pacific hake had proved unsuccessful, but recent advances in tagging technology may facilitate these kinds of studies. Other avenues include developing partnerships with the commercial fishing industry that could be used to gather this information using commercial vessels or by utilizing emerging broad-scale acoustic sampling technologies (Makris et al., 2006). Directly quantifying spawning location and biomass by surveying likely areas would yield important insights into distributional changes and recruitment patterns.

5) Explore possible scenarios of future Pacific hake abundance, distribution, and growth to predict possible impacts in the CCLME. This effort should employ a combination of stock assessment models and food web models in simulations of possible future climate-ocean conditions.

6) Investigate the use of Pacific hake as an indicator species to biological changes in the CCLME, particularly in the face of changing climate-ocean conditions (e.g. King, 2005; The Pacific Coast Ocean Observing System, http://www.pacoos.org/). Pacific hake may be an appropriate species for such monitoring, both because of the sensitivity of its distribution to changes in ocean conditions and its ecological and commercial importance in the CCLME.

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Long-term Trends in Catch Composition
from Elasmobranch Derbies in Elkhorn Slough, California

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Introduction

Elkhorn Slough is a shallow, seasonal estuary of about 1,200 ha at the center of Monterey Bay on the central California coast (Fig. 1). The slough extends approximately 11 km inland from Monterey Bay and is characterized by a main central channel with branching tidal creeks bordered by extensive tidal mudflats and salt marsh. A large portion of the southeastern part of Elkhorn Slough is the Elkhorn Slough National Estuarine Research Reserve (ESNERR). The reserve is managed by the Califor-

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nia Department of Fish and Game and is one of 26 Federally protected estuaries that are part of the National Oceanic and Atmospheric Administration's National Estuarine Research Reserve System. The slough is a highly productive system which supports a diverse array of fishes, invertebrates, marine mammals, and birds.

In 1946, the Pajaro Valley Rod and Gun Club (PVRGC) initiated a late spring-early summer angling derby for elasmobranchs in Elkhorn Slough. The PVRGC was soon joined by the Castroville Rod and Gun Club (CRGC) and the Izaak Walton League (IWL), who sponsored additional annual "shark derbies" at about the same time of the year. The revenues from the derbies helped fund the activities of the clubs. Additionally, the fishermen believed these derbies could help control shark and ray populations that were suspected of reducing more lucrative shellfish and finfish populations in the slough.

While the attendance at each derby fluctuated over the years, the number of boats was usually between 100 and 150, each carrying 2 or 3 fishermen. Many prizes were given away at each derby, including small boats, outboard motors, fishing and hunting equipment, and up to $1,000 in cash at the later derbies. By the early 1980's, only the PVRGC continued to hold the annual angling derby. In addition to the angling derbies, an archery derby for elasmobranchs in Elkhorn Slough was initiated in the mid 1980's and continued until the mid 1990's, but it took only a small fraction of the elasmobranchs that were caught in the angling derbies. Until the early 1990's, little regulation of recreational shark fishing existed in California, and there were no bag limits.

Ichthyologists, most notably the late Earl S. Herald of the California Academy of Sciences in San Francisco, took an early interest in these derbies as a means of collecting data on estuarine elasmobranch populations. From 1951 to 1962, Herald and several colleagues monitored and collected data at the Elkhorn Slough shark derbies. Catch

ABSTRACT—Long-term trends in the elasmobranch assemblage of Elkhorn Slough, Monterey Bay, California, were analyzed by documenting species composition and catch per unit effort (CPUE) from 55 sport fishing derbies that occurred during May, June, and July, from 1951 until 1995. The most abundant species (bat ray, Myliobatis californica; shovelnose guitarfish, Rhinobatos productus; and leopard shark, Triakis semifasciata) were also analyzed for size-weight relationships, trends in size class distribution, stage of maturity, and sex ratios. Changes in species composition over the course of the derbies included the near complete disappearance of shovelnose guitarfish by the 1970's and a slight increase

in the abundance of minor species (mainly smoothhounds, Mustelus spp., and thornback, Platyrhinoidis triseriata) starting in the mid 1960's. The relative abundance of bat rays in the catch steadily increased over the years while the relative abundance of leopard sharks declined during the last two decades. However the average number of bat rays and leopard sharks caught per derby declined during the last two decades. Fishing effort appeared to increase over the course of the derbies. There were no dramatic shifts in the size class distribution data for bat rays, leopard sharks, or shovelnose guitarfish. The catch of bat rays and leopard sharks was consistently dominated by immature individuals, while the

catch of shovelnose guitarfish was heavily dominated by adults. There was evidence of sexual segregation in either immature or mature fish in all the species. Female bat rays and shovelnose guitarfish were larger than their male counterparts and outnumbered males nearly 2:1. Female and male leopard sharks were more nearly equal in size and sex ratio. Changes in species composition are likely due to fishing pressure, shifts in the prevailing oceanographic conditions, and habitat alteration in Elkhorn Slough. The sex ratios, stage of maturity, and size class distributions provide further evidence for the theory that Elkhorn Slough functions as a nursery habitat for bat rays and leopard sharks.

composition and fishing effort were assessed, in addition to individual specimen size, weight, sex, stomach content, and stage of sexual maturity (Herald and Dempster, 1952; Herald, 1953; Herald et al., 1960). In 1963 and 1964, the PVRGC and CRGC collected similar data from their respective derbies along the above format.

Collection of data from the elasmobranch derbies was sporadic in the late 1960's. In 1971, scientists from the Moss Landing Marine Laboratories (MLML), California Department of Fish and Game, California Academy of Sciences, Stanford University, and San Francisco State University resumed the data collection. By 1980, as part of their training in fisheries research, the task had become an annual routine for graduate students at the MLML Ichthyology Laboratory.

In order to minimize the impact of the derbies on the elasmobranchs of Elkhorn Slough and to assist in various research projects, a tag-and-release program was initiated in 1988 through a cooperative effort between MLML, the PVRGC, Monterey Bay Aquarium, and the Elkhorn Slough Foundation. That tagging effort continued until the derbies ended. The 1990's saw increasing environmental awareness in the general public and protests from environmental groups regarding shark conservation in Elkhorn Slough, as well as waning interests on the part of the derby organizers and sponsors. As a result the final shark derby was held on 16 July 1995 and there have been none since.

Seven species of elasmobranchs are typically found in Elkhorn Slough. These include: bat ray, *Myliobatis californica*; shovelnose guitarfish, *Rhinobatos productus*; leopard shark, *Triakis semifasciata*; gray smoothhound, *Mustelus californicus*; brown smoothhound, *Mustelus henlei*; thornback, *Platyrhinoidis triseriata*; and round stingray, *Urobatis halleri*. In addition, the Pacific electric ray, *Torpedo californica*; spiny dogfish, *Squalus acanthias*; and big skate, *Raja binoculata*, have been found in Elkhorn Slough. All but Pacific electric rays were caught during the derbies. A number of studies have been conducted on the feeding ecology (Ackerman, 1971; Talent, 1976; Talent, 1982; San Filippo, 1995; Barry et al., 1996; Kao, 2000), reproduction (Ackerman, 1971; Talent, 1985; Martin and Cailliet, 1988a), and age and growth (Ackerman, 1971; Martin and Cailliet, 1988b; Yudin and Cailliet, 1990; Kusher et al., 1992) of these elasmobranchs in Elkhorn Slough.

Elasmobranch species composition and seasonal patterns of occurrence in Elkhorn Slough have been documented by Barry (1983), Talent (1985), Yoklavich et al. (1991), and San Filippo (1995) although Talent (1985) was the only one to focus on the entire elasmobranch assemblage. Talent (1985) found that leopard sharks and bat rays were the two most common species, comprising 56% and 20% of the catch, respectively, and were commonly caught year-round though in slightly lower numbers in the winter.
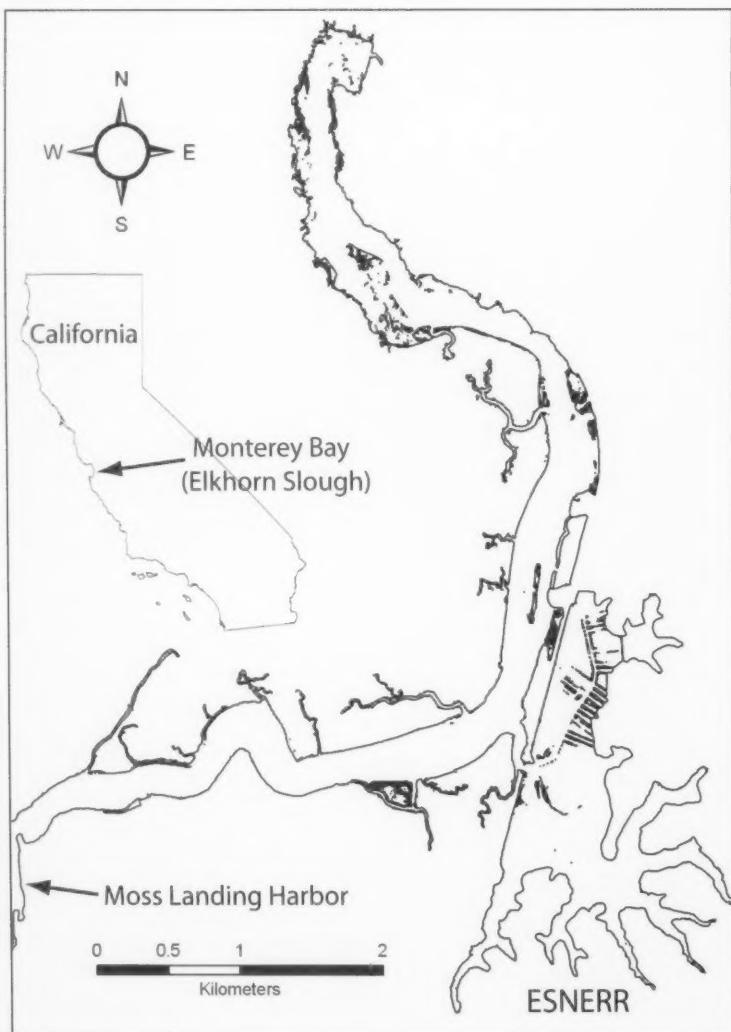

Figure 1.—Elkhorn Slough, California. ESNERR is the Elkhorn Slough National Estuarine Research Reserve.

Talent (1985) believed that the bat ray catch was not necessarily representative of their abundance in the slough, due to the difficulties of catching bat rays in his sampling gear (gill nets). Other species had more pronounced seasonal occurrences and were caught in lower numbers. Gray smoothhounds (9%) and round stingrays (6%) were most abundant during the winter. Shovelnose guitarfish (5%) were most abundant during the fall, and brown smoothhounds (3%) were most abundant during the spring.

Barry (1983) found that in shallow marsh habitats of the slough leopard sharks and bat rays were the only elasmobranchs caught in significant numbers, especially during the spring and summer, and that they were primarily juveniles with fewer reproductively active adults. Yoklavich et al. (1991) also found that leopard sharks and bat rays were the only two elasmobranchs caught in significant numbers, and that juvenile and reproductively mature adult leopard sharks and bat rays were most abundant in the spring and summer, with fewer leopard sharks and young bat rays found in the winter. Leopard sharks and bat rays were categorized as being partial residents of Elkhorn Slough, meaning that they primarily live in the slough, seasonally or ontogenetically move to the ocean, and return to reproduce in the slough. They also categorized the round stingray and gray smoothhound as being marine, meaning that they are a coastal species rarely found in Elkhorn Slough.

San Filippo (1995) found slightly different patterns than those found in previous studies. Gray smoothhounds were the most abundant elasmobranch caught, comprising 71% of the catch. Bat rays made up 15% of the catch, leopard sharks 6%, shovelnose guitarfish 5%, thornbacks 2.5%, and round stingrays 0.5%. The abundance of gray smoothhounds was lowest in the late fall and winter months. Differences between San Filippo (1995) and the other studies is likely a result of different methods and sampling areas, habitat alteration, plus the extended period of time that passed between studies. San Filippo (1995) sampled in ESNERR in the early 1990's using only a beach seine. Barry (1983), Talent (1985), and Yoklavich et al. (1991) all sampled between 1971 and 1980 primarily using a mix of gill nets and otter trawls, and they all sampled in the main channel and major tidal creeks.

These patterns of abundance may be related to prey availability, reproduction, or the physical environment (Ackerman, 1971; Talent, 1976; Talent, 1982; Barry, 1983; Talent, 1985; Martin and Cailliet, 1988a; San Filippo, 1995; Hopkins and Cech Jr., 2003). Reproduction is likely a major factor in these patterns of seasonal abundance. Elkhorn Slough is believed to function as a nursery area for several elasmobranchs, such as the leopard shark (Ackerman, 1971; Barry, 1983; Talent, 1985), bat ray (Barry, 1983; Talent, 1985; Martin and Cailliet, 1988a), gray smoothhound (San Filippo, 1995), and possibly the shovelnose guitarfish (Herald et al., 1960). There is also some evidence that thornbacks also may currently use Elkhorn Slough as a nursery area, but this has not been confirmed (Carlisle[1]).

These studies provide periodic information on the structure and seasonality of the elasmobranch assemblage in Elkhorn Slough. They function primarily as independent snapshots of species composition and biological characteristics based on various sampling methods in different parts of the slough. Assessing long-term changes in the elasmobranch assemblage requires more consistent sampling over an extended period of time. Short-term, independent studies that use various types of sampling gear, different objectives, and sample different habitats within Elkhorn Slough are of value, but they are not the best way to characterize long-term trends, either independently or collectively

This study was done to assess long-term trends in elasmobranch catch composition and catch per unit effort (CPUE) from data collected during Elkhorn Slough shark derbies from 1951 to 1995. In addition, size and weight relationships, size class distributions, stage of maturity, and sex ratios were determined for bat rays, shovelnose guitarfish, and leopard sharks. The use of such a long-term and unique data set provides a rare opportunity to track changes in the composition and population structure of elasmobranchs in a coastal estuary.

Methods and Materials

Field Collection

Elasmobranch catch data from 55 shark derbies in Elkhorn Slough were collected by various researchers, as well as the derby organizers themselves, from 1951 through 1995 (Table 1). Usually there was only one derby per year, but in some years, there were two derbies or none at all. Prior to 1988, data were collected at a single weigh-in station at the mouth of the slough in Moss Landing Harbor. Starting in 1988 and continuing until the end of the derbies, elasmobranchs were also sampled at roving weigh-in stations on boats staffed primarily by MLML graduate students. The purpose of the on-the-water stations was to reduce fishing mortality and conduct tagging/mark-recapture studies. Over the years, besides being weighed, total length (leopard sharks, brown/gray smoothhounds, shovelnose guitarfish, and thornbacks) or disk width (bat rays) for many individuals was also measured.

We assume that the elasmobranch catch was fully and accurately reported and that this is representative of the elasmobranch assemblage in the slough during a given derby. Because different species, sexes, and size classes may have different feeding ecologies (feeding habits, feeding chronology, frequency of feeding, susceptibility to capture, etc.), these data may not necessarily represent the relative abundance of each species or the exact nature of the population structure of a given species in the slough during the derbies. In addition, it is possible that there were gear biases or problems with the reporting of the catch by fishermen, such as under reporting small individuals or species.

[1]Carlisle, A. 2004. Hopkins Marine Station, Stanford Univ., Pacific Grove, Calif. Personal observ.

However, we believe that there is no evidence that there were systematic problems with the reporting of the catch, or that the different feeding ecologies of the different species influenced the accuracy of the data. Our confidence in the data is due to the fact that the species composition did not vary significantly from derby to derby and that the catch of each species was composed of individuals of all size ranges and both sexes. Despite potential issues with the data, this 44-year data set is extremely valuable, especially due to its unique ability to assess elasmobranch populations in Elkhorn Slough during the late spring and early summer over a long period of time.

Table 1.—Elkhorn Slough elasmobranch derbies sampled for catch statistics from 1951 to 1995 with derby sponsors, researcher affiliation, and estimated number of fishermen.

Derbies	Sponsors[1]	Researcher affiliation[2]	No. of fishermen
20 May 1951	PVRGC	CAS	237
08 Jun 1952	PVRGC	CAS	308
27 Jul 1952	CRGC	CAS	322
14 Jun 1953	Unknown	CAS	270
28 Jun 1953	Unknown	CAS	351
06 Jun 1954	Unknown	CAS	Unknown
20 Jun 1954[3]	Unknown	CAS	Unknown
05 Jun 1955	Unknown	CAS	Unknown
19 Jun 1955[3]	Unknown	CAS	Unknown
10 Jun 1956[3]	Unknown	CAS	Unknown
24 Jun 1956[3]	CRGC	CAS	60
16 Jun 1957[3]	PVRGC	CAS	600
14 Jul 1957[3]	Unknown	CAS	Unknown
01 Jun 1958	Unknown	CAS	Unknown
15 Jun 1958	Unknown	CAS	Unknown
07 Jun 1959	Unknown	CAS	Unknown
21 Jun 1959	Unknown	CAS	Unknown
12 Jun 1960	Unknown	CAS	Unknown
04 Jun 1961	CRGC	CAS	Unknown
18 Jun 1961	PVRGC	CAS	72
03 Jun 1962	PVRGC	CAS	275
17 Jun 1962	CRGC	CAS	400
23 Jun 1963	PVRGC	PVRGC	Unknown
21 Jun 1964	CRGC	CRGC	Unknown
23 May 1971	Unknown	MLML	Unknown
06 Jun 1971	Unknown	MLML	Unknown
11 Jun 1972	Unknown	MLML	Unknown
25 Jun 1972	Unknown	MLML	Unknown
03 Jun 1973	PVRGC	MLML	Unknown
01 Jul 1973	Unknown	MLML	Unknown
25 May 1975	Unknown	CAS	Unknown
08 Jun 1975	PVRGC	CAS	Unknown
16 May 1976	IWL	CDFG	552
13 Jun 1976	PVRGC	CDFG	515
11 Jun 1978	PVRGC	CDFG	Unknown
25 Jun 1978	IWL	CDFG	Unknown
01 Jun 1980	IWL	MLML	450
15 Jun 1980	PVRGC	MLML	459
14 Jun 1981	PVRGC	MLML	444
05 Jul 1981	IWL	MLML	501
26 Jun 1983	PVRGC	MLML	510
03 Jun 1984	PVRGC	MLML	492
16 Jun 1985	PVRGC	MLML	609
22 Jun 1986	PVRGC	MLML	489
28 Jun 1987	PVRGC	MLML	483
26 Jun 1988	PVRGC	MLML	390
25 Jun 1989	PVRGC	MLML	330
24 Jun 1990	PVRGC	MLML	336
23 Jun 1991	PVRGC	MLML	360
07 Jun 1992	PVRGC	MLML	Unknown
25 Jul 1993	PVRGC	MLML	400
10 Jul 1994	PVRGC	MLML	360
16 Jul 1995	PVRGC	MLML	Unknown

[1] PVRGC = Pajaro Valley Rod and Gun Club; CRGC = Castroville Rod and Gun Club; IWL = Izaak Walton League.

[2] CAS = California Academy of Sciences; CDFG = California Department of Fish & Game; MLML = Moss Landing Marine Labs.

[3] Records on bat ray sizes and weights were lost.

Data Analysis

Catch composition, size class distributions, stage of maturity of the catch, sex ratios, and CPUE were analyzed graphically. Bat rays, shovelnose guitarfish, and leopard sharks were the only species caught in numbers large enough to analyze for shifts in size class distributions, stage of maturity, sex ratios, and to generate length (TL or DW) weight regressions. Length-weight regressions were calculated using specimens that were measured for both length and weight. When only weight or length was known for an individual sample, the other parameter was estimated from the calculated length-weight relationship. Size class distributions, stage of maturity, and sex ratios include both the specimens that were measured and weighed, plus the specimens whose weight or length/disc width were estimated using the calculated length weight regressions.

Catch records for brown and gray smoothhounds were lumped together as *Mustelus* spp. due to the lack of certainty in many of the species identifications. Weight data from the 24 June 1956 derby were not used in our analysis due to suspected poor quality data (i.e. high weight values probably due to an uncalibrated scale). Bat ray disc width and weight data from six derbies during the late 1950's were lost from the original paper files and therefore were not be included in our analyses. In addition, data considered to be suspect (e.g. abnormal weights or lengths) were not included in these analyses due to the likelihood of a measurement or transcription error.

The size at 100% maturity (where all animals above that size were believed to be mature) was used to estimate the proportion of the catch that was mature. We chose this estimate because we felt that this was the more conservative and biologically relevant estimate and because it is the only estimate available for all species. However, this estimate of size at maturity will artificially increase the number of immature animals. This is especially true for bat rays, where females reach first maturity and 100% maturity at 45 cm DW and 100 cm DW

Figure 2.—Species composition of derby landings for the three major species: bat ray, leopard shark, and shovelnose guitarfish. The derbies are listed in chronological order and there are gaps for the years where derbies did not occur. The bar at the top of the graph shows the cool (black) or warm (gray) phases of the Pacific Decadal Oscillation during the time of the derbies based on Mantua and Hare (2002).

respectively, while for males it was 45 cm and 62 cm DW (Martin and Cailliet, 1988a), so there is a large discrepancy between the different estimates, especially for females.

For leopard sharks and shovelnose guitarfish the differences between sizes at first maturity and 100% maturity are not as great. Size at maturity for leopard sharks was based on Kusher et al. (1992), with a size of maturity for males of 105 cm TL and 110 cm TL for females. The size at maturity of shovelnose guitarfish was based on Timmons and Bray (1997), with males maturing at 100 cm TL and females at 99 cm TL. The studies that were used to estimate the size at maturity for leopard sharks and bat rays were conducted in Elkhorn Slough, but the study of shovelnose guitarfish was conducted in southern California.

Results

Catch Composition

A total of 5,954 elasmobranchs were sampled from the 55 derbies that oc-

curred between 1951 and 1995. Four derbies occurred in May, 44 in June, and 7 in July. As a result, these data are primarily representative of elasmobranch populations in Elkhorn Slough in June. Of the total catch, 3,310 (55.6%) were bat rays, 1,544 (25.9%) were leopard sharks, 863 (14.5%) were shovelnose guitarfish, 113 (1.9%) were smoothhounds, 94 (1.6%) were thornbacks, 25 (0.4%) were round stingrays, 4 (0.1%) were spiny dogfish, and 1 was a big skate. These are the first records of spiny dogfish and big skates in Elkhorn Slough. One spiny dogfish was caught in both the 13 June 1976 and 28 June 1987 derbies, and two were caught in the 23 June 1991 derby; the big skate was caught in the 23 June 1991 derby. The three most common species (bat ray, leopard shark, and shovelnose guitarfish) comprised more than 90% of the catch in most individual derbies and 96% of the cumulative derby catch, with bat rays being the most abundant species in nearly every derby.

Over the period of this study, several shifts occurred in the elasmobranch

species composition (Fig. 2, 3). The most obvious change has been the relative disappearance of shovelnose guitarfish from the catch. During the 1950's, shovelnose guitarfish were the second most abundant species, averaging about 28% of the catch. In those years, the shovelnose guitarfish even surpassed the number of bat rays caught in some derbies. However the relative abundance of shovelnose guitarfish declined steadily, and by the early 1970's their numbers had dropped considerably to about 5% of the catch. By the 1990's they composed about 3% of the catch. The average number landed per derby declined from around 38 fish per derby in the 1950's to around 3 per derby by the 1990's (Table 2).

The relative abundance of bat rays has steadily increased from 47% in the 1950's to 68% in the 1990's. While the relative abundance has increased, the number landed has decreased from an average of 63 fish per derby in the 1950's to around 50 fish per derby in the 1990's. The relative abundance of
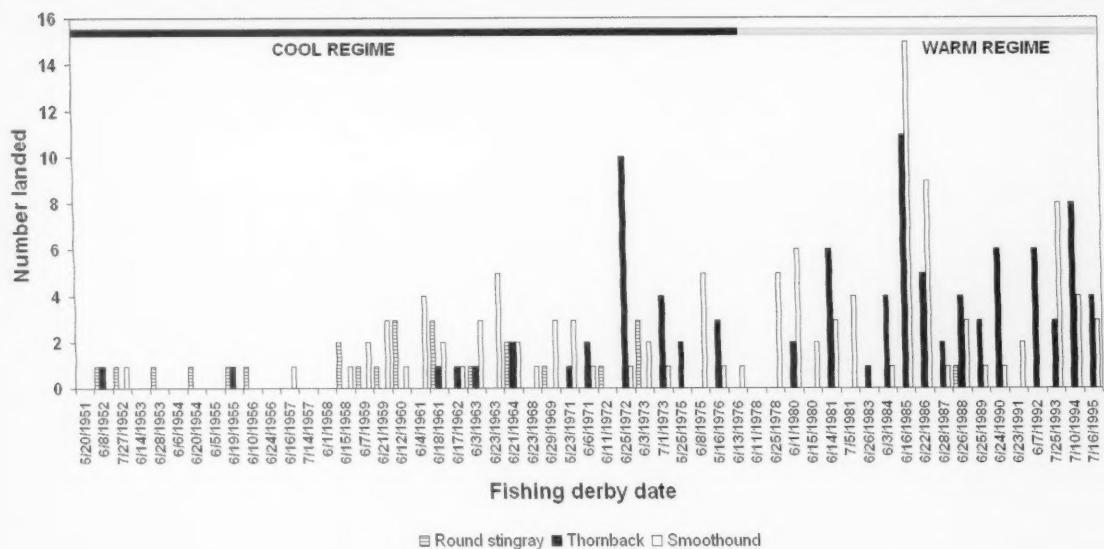
Figure 3.— Species composition of derby landings for the three minor species: round stingray, thornback, and smoothhound. The derbies are listed in chronological order and there are gaps for the years where derbies did not occur. The bar at the top of the graph shows the cool (black) or warm (gray) phases of the Pacific Decadal Oscillation during the time of the derbies based on Mantua and Hare (2002).

Table 2.—Average proportion of total catch, stage of maturity, and sex ratios grouped by decade. Values are the mean and standard error (SE) for all of the derbies occurring in that decade. In the total landed column, the number in brackets (No. with data) refers to the number of animals that were used in estimating the stage of maturity and sex ratios. Fewer animals were used to estimate maturity and sex ratios than were caught due to data being lost or incomplete. All data from a particular species were pooled together to calculate values shown in "overall" rows. For shovelnose guitarfish the entire catch of the 1980's and 1990's were grouped due to the low numbers that were caught.

	Decade	Total landed (No. with data)	Avg. landed per derby (SE)	Avg. proportion of total catch (SE)	Avg. proportion mature (SE)	Avg. immature ♀/♂ sex ratio (SE)	Avg. mature ♀/♂ sex ratio (SE)	Avg. overall ♀/♂ sex ratio (SE)
Bat rays	1950's	1,071 (580)	63.00 (±6.10)	0.47 (±0.02)	0.33 (±0.02)	2.97 (±0.37)	0.84 (±0.17)	1.77 (±0.20)
	1960's	534 (522)	59.30 (±13.30)	0.55 (±0.07)	0.33 (±0.02)	4.61 (±1.18)	0.98 (±0.19)	2.09 (±0.22)
	1970's	787 (765)	65.60 (±6.60)	0.61 (±0.04)	0.32 (±0.04)	4.05 (±1.01)	1.01 (±0.20)	1.93 (±0.21)
	1980's	616 (565)	56.00 (±4.40)	0.64 (±0.03)	0.38 (±0.05)	7.98 (±3.77)	2.03 (±0.51)	4.05 (±1.06)
	1990's	302 (291)	50.30 (±9.80)	0.68 (±0.02)	0.35 (±0.04)	10.10 (±3.96)	1.86 (±1.04)	4.84 (±2.02)
	Overall	3,310 (2723)	60.20 (±3.40)	0.57 (±0.02)	0.35 (±0.02)	5.64 (±1.09)	1.30 (±0.19)	2.65 (±0.34)
Leopard shark	1950's	545 (526)	32.10 (±4.50)	0.24 (±0.03)	0.39 (±0.04)	1.05 (±0.16)	0.82 (±0.14)	0.96 (±0.14)
	1960's	262 (217)	29.10 (±5.00)	0.28 (±0.05)	0.26 (±0.05)	1.45 (±0.39)	1.17 (±0.43)	1.15 (±0.14)
	1970's	409 (390)	34.10 (±4.60)	0.31 (±0.03)	0.31 (±0.05)	0.96 (±0.20)	1.90 (±0.78)	0.84 (±0.10)
	1980's	247 (216)	22.40 (±3.80)	0.25 (±0.04)	0.29 (±0.05)	1.68 (±0.40)	1.35 (±0.31)	1.32 (±0.14)
	1990's	81 (77)	13.50 (±3.10)	0.18 (±0.02)	0.34 (±0.08)	1.08 (±0.22)	6.08 (±2.08)	1.87 (±0.48)
	Overall	1,544 (1426)	28.10 (±2.20)	0.26 (±0.02)	0.33 (±0.02)	1.23 (±0.12)	1.66 (±0.32)	1.13 (±0.09)
Shovelnose guitarfish	1950's	639 (577)	37.60 (±4.90)	0.28 (±0.03)	0.84 (±0.02)	1.03 (±0.16)	3.09 (±0.58)	2.19 (±0.26)
	1960's	125 (109)	13.90 (±2.90)	0.12 (±0.02)	0.64 (±0.06)	2.36 (±0.54)	2.95 (±0.94)	2.83 (±1.04)
	1970's	63 (48)	5.30 (±1.10)	0.05 (±0.01)	0.81 (±0.12)	0.17 (±0.17)	0.95 (±0.27)	0.68 (±0.17)
	1980's	20 (14)	1.80 (±0.70)	0.02 (±0.01)	0.64	0.67	8.00	2.50
	1990's	16 (17)	2.70 (±1.30)	0.03 (±0.01)	0.71	0.67	1.40	1.13
	Overall	863 (765)	15.70 (±2.60)	0.12 (±0.02)	0.76 (±0.04)	1.12 (±0.21)	2.57 (±0.39)	1.84 (±0.28)

leopard sharks fluctuated over the years but remained the second most abundant species caught in the derbies, comprising about 25% of the total catch.

Leopard sharks exhibited a gradual increase in relative abundance from 24% of the catch in the 1950's to 31% of the catch in the 1970's. However, during the 1980's and 1990's, the relative abundance of leopard sharks declined and by the 1990's it was approximately 18% of the catch. The average number of leopard sharks landed per derby showed the same pattern, ranging from 29 to 34 fish from the 1950's to the 1970's, but the average number of leopard sharks declined to about 22 and 13 fish per derby in the 1980's and 1990's, respectively.

The frequency of occurrence and relative abundance of thornback and
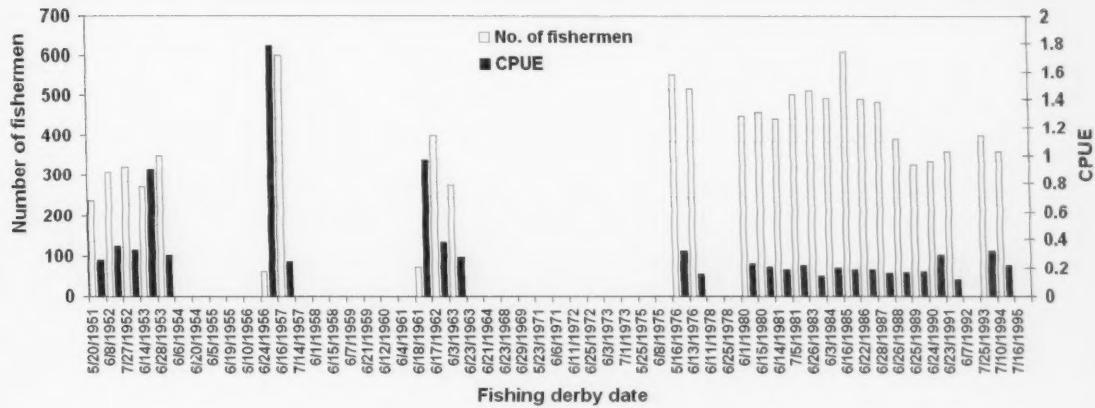
Figure 4.—Number of derby fishermen by derby date and their CPUE.

smoothhounds increased in later derbies compared to the derbies in the 1950's and 1960's, but they continued to comprise only a small percentage of the catch. Round stingray were never caught in significant numbers, but nearly all of them were caught between 1951 and 1973.

Catch Per Unit of Effort

Fisherman numbers at individual derbies are only available for 27 out of the 55 derbies. These data were collected intermittently during the early years but were collected relatively consistently from the 1980's to the end of the derbies (Table 1). The number of fishermen generally increased as the derbies progressed, averaging 277.5 ± 60.29 (SE) for the first decade (1951–61) to 417.4 ± 30.74 (SE) in the last decade (1985–95), up 50.4%. Fewer fishermen participated during the first half of the derbies (1951–73, mean = 290 ± 49.1 (SE)) than during the last half of the derbies (1974–95, mean = 452 ±19.2 (SE)), and the overall average was 392 ±26.2 (SE) fishermen/derby.

The fewest fishermen recorded (attributed to bad weather) was 60 at the 24 June 1956 derby, and the greatest number was 609 at the 16 June 1985 derby. Also, elasmobranch landings per decade decreased steadily, with average

landings of 133.8, 106.4, 108.8, 88, and 74.5 from the 1950's to 1990's, respectively. The average landings declined from 135 ±10.255 (SE) during the first decade (1951–61) to 77.4 ±8.305 (SE) for the last decade (1985–95), down 42.7%.

CPUE was higher and more variable during the first two decades (Fig. 4) after which it declined, and it was relatively low and stable during the 1980's and 1990's. There were three peaks in the CPUE during the 14 June 1953, 24 June 1956, and 18 June 1961 derbies. Two of those peaks (24 June 1956 and 18 June 1961) were the two derbies with the lowest number of fishermen (60 and 72, respectively), and the other peak was during the 14 June 1953 derby with 270 fishermen. During the first 22 years of derbies, the average CPUE was 0.581 ±0.16 (SE) fish/fisherman (0.31 ±0.02 (SE) when the peaks are not included), while for the second half it was 0.205 ±0.014 (SE).

Size-Weight Relationships

Male bat rays had a disc width-weight relationship of $y = 2.02671e{-}08x^{2.97357}$ ($r^2 = 0.95$) and female bat rays had a disc width-weight relationship of $y = 1.03747e{-}08x^{3.08729}$ ($r^2 = 0.96$) (Fig. 5). Male leopard sharks had a length-weight relationship of $y = 5.13e{-}09x^{2.95917}$ ($r^2 = 0.96$) and female leopard sharks

had a length-weight relationship of $y = 2.67e{-}009x^{3.06261}$ ($r^2 = 0.96$) (Fig. 6).

Male and female shovelnose guitarfish exhibited more variability in their growth regressions than the other species. Male shovelnose guitarfish had a length-weight relationship of $y = 1.83739e{-}08x^{2.76348}$ ($r^2 = 0.81$) and female shovelnose guitarfish $y = 5.37655e{-}09x^{2.96729}$ ($r^2 = 0.89$) (Fig. 7). Smaller size classes of shovelnose guitarfish were underrepresented in the data, so their regression calculations were not as robust as the bat rays or leopard sharks.

Size Class Distributions

Bat rays (Fig. 8), leopard sharks (Fig. 9), and shovelnose guitarfish (Fig. 10) showed no dramatic size frequency shifts over the course of the derbies. The size of female bat rays may have increased slightly since the average disc width of females was slightly larger during the 1980's and 1990's. There were always very few of the smaller shovelnose guitarfish, but they had disappeared almost completely by 1970. The average size of male and female leopard sharks was slightly larger in the 1950's than in following decades. Female bat rays and shovelnose guitarfish in Elkhorn Slough attained a larger size than their male counterparts, while male

and female leopard sharks were of a similar size.

Stage of Maturity

Bat ray catches were dominated by immature individuals, specifically immature females (Table 2). Based on Martin and Cailliet's (1988a) estimate of size at 100% maturity for females and males, between 60 and 70% of the catch was immature. Even with the potential bias due to the size at maturity estimate used, the average size of the female bat catch (78.9 cm DW, which is 100 mm smaller than size at 50% maturity (88.1 cm DW)), indicates that the majority of females were immature. The proportion of mature bat rays ranged from an average of 32% in the 1970's to 38% in the 1980's, and averaged 35% overall. The proportion of mature leopard sharks caught varied more than in bat rays, ranging from an average of 26% in the 1960's to 39% in the 1950's, with an overall average of 33%. Unlike bat rays and leopard sharks, the majority of shovelnose guitarfish caught were mature (average of 63% in the 1960's to 84% in the 1950's, with an overall average of 76%).

Sex Ratios

The sex ratios of the total catch showed that both bat rays (Fig. 11) and shovelnose guitarfish (Fig. 12) exhibited a similar trend in which females generally outnumbered males by a ratio of two to one. The sex ratio for all the bat rays caught during the derbies was 1.9:1 ($\female$:$\male$), while for shovelnose guitarfish it was 1.8:1 ($\female$:$\male$). However, for bat rays, this sex ratio was primarily due to the large number of immature females since the sex ratio of mature rays was closer to 1:1 ($\female$:$\male$). The numbers of female and male leopard sharks were more evenly balanced (Fig. 13), with an overall sex ratio of 0.96:1 ($\female$:$\male$).

The sex ratios, grouped by decade and stage of maturity, showed that bat ray, leopard shark, and shovelnose guitarfish catches were generally dominated by females. The sex ratio of immature bat rays was heavily skewed towards females (ranging from a sex ratio of 2.97:1 ($\female$:$\male$) in the 1950's to 10.1:1 ($\female$:$\male$) in the 1990's), while for adults it was closer to 1:1 ($\female$:$\male$), except for the 1980's and 1990's when it was closer to 2:1 ($\female$:$\male$) (Table 2). Both immature and mature leopard sharks had a sex ratio closer to 1:1 ($\female$:$\male$) than bat rays, but females usually were more abundant than males. Overall, the catches of mature leopard sharks were more dominated by females than were immature animals, and while most of the ratios were slightly greater than 1:1 ($\female$:$\male$), they were as high as 6.08:1 ($\female$:$\male$) in the 1990's. Adult shovelnose guitarfish catches were

A

$$y = 2.02671e\text{-}08x^{2.97357} \quad r^2 = 0.9496 \quad n = 623$$

size range = 219 - 1,280 mm DW

B

$$y = 1.03747e\text{-}08x^{3.08729} \quad r^2 = 0.9564 \quad n = 1,334$$

size range = 260 - 1,540 mm DW
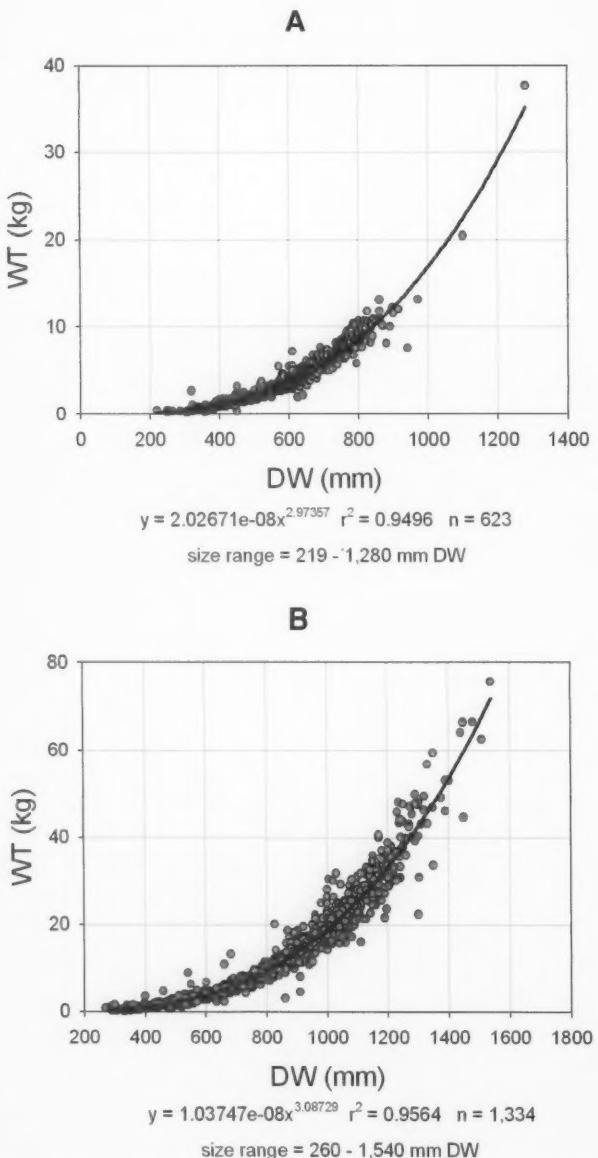
Figure 5.—Disc width-weight regression for A) male bat rays and B) female bat rays.

consistently dominated by females until the 1970's and 1990's, when the ratio was closer to 1:1 ($\female$:$\male$). Sex ratios of immature shovelnose guitarfish were less dominated by females than were adults, and during the 1970's–90's males dominated.

Minor species (thornback, round stingray, and smoothhounds) numbers were insufficient to examine sex ratio by individual derby, decade, or stage of maturity, but the sex ratio for these species was calculated for the overall catch. The overall sex ratio of the thornback was strongly dominated by females at 6.75:1 ($\female$:$\male$). The overall sex ratio of the round stingray was strongly dominated by males at 0.31:1 ($\female$:$\male$), and the overall smoothhound sex ratio was 1.5:1 ($\female$:$\male$).

Discussion

Elkhorn Slough has undergone substantial changes over the last 150 yr due to human activity, mainly through diking of marshland for agricultural purposes, channel construction for habitat restoration, and destruction of levees (Van Dyke and Wasson, 2005). The most dramatic period of change started in 1946–47 when the U.S. Army Corps of Engineers dredged a channel to make Moss Landing Harbor. This opened Elkhorn Slough, once a sluggish wetland system with muted tides, to direct tidal flow, greatly increasing erosion and changing it from a depositional to an erosional area (Caffrey and Broenkow, 2002). In addition, several diked areas were reopened to tidal flow during the following decades. This included the creation of the ESNERR marsh restoration site in 1983, which increased the wetted area of the slough by 20% and increased the total volume of the slough by 30% (Malzone and Kvitek[2]). These habitat changes have likely influenced the composition of elasmobranch populations in Elkhorn Slough.

In total, the tidal volume of Elkhorn Slough increased by over 200% since

A

$y = 5.13e\text{-}09x^{2.95917}$ $r^2 = 0.9563$ $n = 498$

size range = 262 - 1,410 mm TL

B

$y = 2.67e\text{-}009x^{3.06261}$ $r^2 = 0.9581$ $n = 476$

size range = 200 - 1,481 mm TL
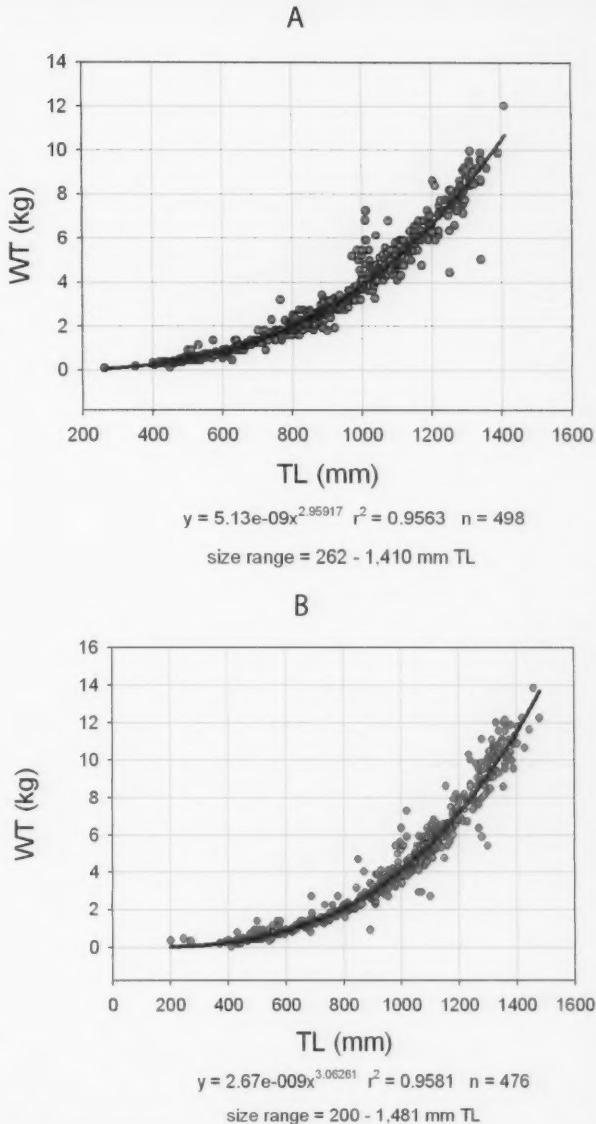
Figure 6.—Length-weight regression for A) male leopard sharks and B) female leopard sharks.

1947 (Crampton, 1994; Malzone, 1999). As a result, Elkhorn Slough has been transformed into a highly tidal embayment with a significant amount of tidal scour causing erosion in the main channel, tidal creeks, mudflats, and bordering salt marsh (Malzone, 1999; Caffrey and Broenkow, 2002; Van Dyke and Wasson, 2005). Channels and tidal creeks have become wider and deeper (the average cross sectional width of tidal creeks has increased from 2.5 m in 1931 to 12.4 m in 2003), salt marsh has converted to mudflats, existing mudflats have been eroded to lower tidal levels, and degraded marshland and mudflats are now

the primary habitats in Elkhorn Slough (Van Dyke and Wasson, 2005). Since the 1970's the substrate has shifted from a more unconsolidated soft bottom towards a more consolidated clay bottom (Lindquist, 1998). The onset of these changes and disruption of ecological processes (e.g. hydrology, habitat type) in 1947 corresponded closely with the onset of the derbies in 1946.

These alterations have changed the type and amount of habitat available for elasmobranchs and almost certainly the diversity and availability of prey.

Yoklavich et al. (2002) reported that the changes to Elkhorn Slough have impacted the species composition, abundance, and trophic patterns of the ichthyofaunal assemblage of the slough through such processes as changing prey availability and habitat alteration. Teleosts have been directly affected by these changes, with their diets being less diverse in the 1990's than in the 1970's, due to the lower diversity and density of the invertebrate assemblage in the slough which resulted from erosion (Lindquist, 1998; Yoklavich et al., 2002). The diet of leopard sharks has similarly shifted as a result of habitat alteration. In the 1970's leopard sharks had a more diverse diet than they do currently and they exhibited an ontogenetic shift in diet (Talent, 1976). Kao (2000) found that the diets of leopard sharks are less diverse than they were in the 1970's and that the ontogenetic shift was no longer apparent as the diets of both small and large sharks converged on a smaller number of prey. Because they likely compete directly with elasmobranchs for certain prey items (Kao, 2000), the reestablishment of sea otters may also have impacted the elasmobranchs of Elkhorn Slough.

In addition to diet changes, the alteration has likely had a direct effect on the function of the slough as a nursery area for elasmobranchs. Barry (1983) found that leopard sharks likely used the shallow tidal creeks and mudflats of the slough as nursery areas. Those tidal creeks and mudflats have since experienced significant amounts of erosion, becoming wider and deeper so it is likely that their function as a nursery area has changed. The fact that the spiny dogfish and big skate were all caught during the later years demonstrates how the slough has changed from a sluggish backwater wetland to an open tidally influenced embayment that is more accessible to coastal marine species.

Changes in the prevailing oceanographic conditions could also affect the elasmobranch assemblage of Elkhorn Slough. There is strong interannual to interdecadal variability in the climate in the Pacific Basin, which leads to warm or cool climatic regimes (Mantua and

A

$$y = 1.83739e\text{-}08x^{2.76348} \quad r^2 = 0.8093 \quad n = 154$$

size range = 531 - 1,195 mm TL

B

$$y = 5.37655e\text{-}09x^{2.96729} \quad r^2 = 0.8935 \quad n = 265$$

size range = 370 - 1,454 mm TL
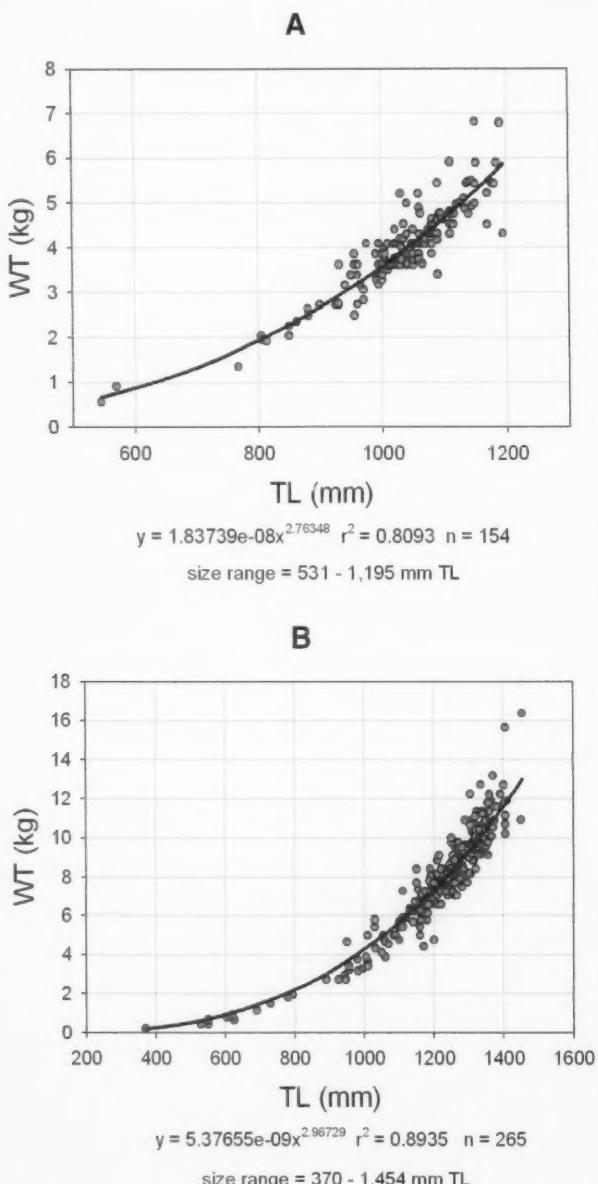
Figure 7.—Length-weight regression for A) male shovelnose guitarfish and B) female shovelnose guitarfish.

Hare, 2002). This is often called the Pacific Decadal Oscillation (PDO). It has been described as a long-lived El Niño-like pattern of Pacific climate variability because they have very similar climatic effects but are very different in duration.

These regimes are longer in duration than El Niño, usually lasting for several decades. In addition to several other climatic characteristics, warm PDO phases (warm regimes) are characterized by anomalously cool sea surface temperatures and increased productivity in the central North Pacific and anomalously warm temperatures and decreased productivity along the west coast of the Americas. The inverse is true during cool PDO phases (cool regimes).

There have been two full PDO cycles over the last century. Cool regimes existed from 1890–24 and 1947–76 and warm regimes occurred from 1925–46 and from 1977 to the late 1990's (Mantua and Hare, 2002). These regime shifts are reported to have a dramatic effect on Pacific marine ecosystems. The abundance of plankton, fishes, marine mammals, and birds have all been shown to track these shifts, with certain suites of species or assemblages being abundant during warm regimes and others more abundant during cool regimes (Francis et al., 1998; Beamish et al., 1999; Mantua and Hare, 2002).

Bat Rays

The average number of bat rays landed per derby decreased in the 1980's and 1990's, and this could indicate a decrease in the abundance of bat rays in Elkhorn Slough. This decline could be due to habitat alteration, fishing pressure, or regime shifts, although it is unlikely that regime shifts would impact the abundance of bat rays since Monterey Bay is in the middle of their range. It is more likely that habitat alteration and fishing pressure are responsible for any possible decline in bat ray abundance.

Habitat alteration, which has been well documented in Elkhorn Slough (Crampton, 1994; Malzone, 1999; Caffrey and Broenkow, 2002; Van Dyke and Wasson, 2005), could impact the
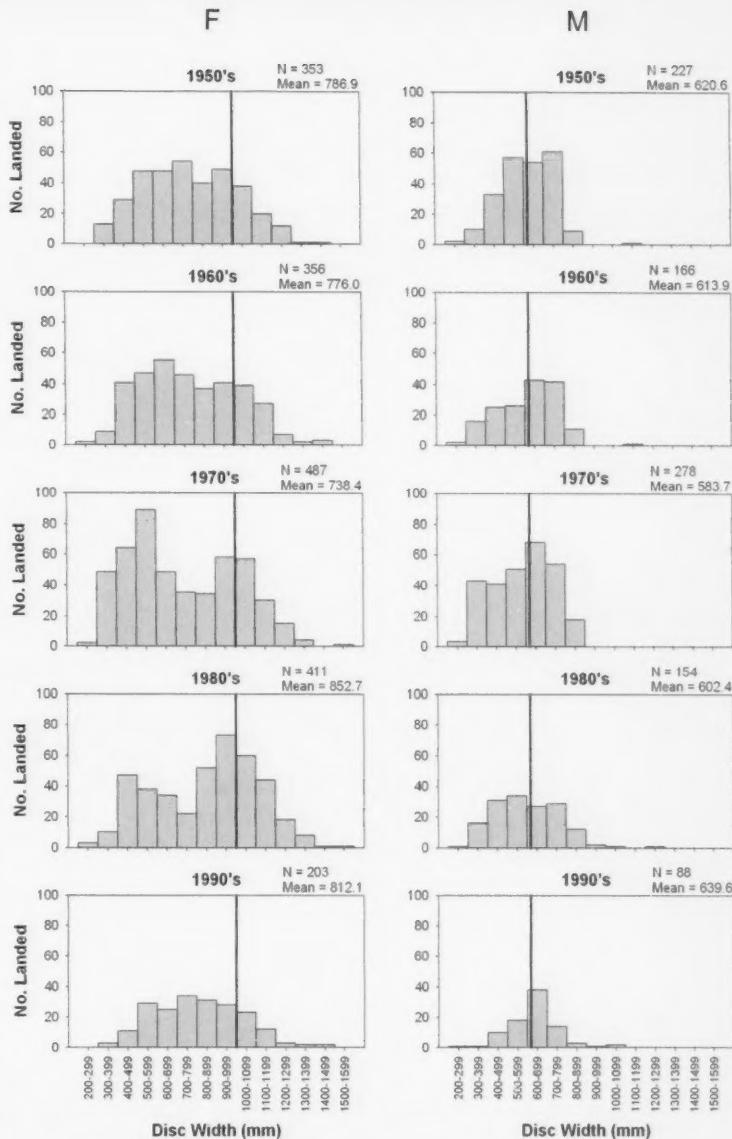

Figure 8.—Size class distribution of male and female bat rays by decade. The vertical line indicates size at 100% maturity.

abundance of bat rays through a number of mechanisms. It could alter prey availability (as documented by Kao (2000) for leopard sharks and Lindquist (1998) for teleosts) or impact the type and availability of habitats used by juveniles and adults. In addition it could alter the function of the slough as a nursery area.

Fishing pressure also could impact their abundance. The decrease in abundance appears to correspond with the increase in fishing pressure which appears to have started in the second half of the derbies, although due to gaps in the fishing effort data this is speculative. Herald (1953) suggested that bat rays

were more residential than other species of elasmobranchs in the slough, and as a result they might be more susceptible to overfishing.

However, based on our current understanding of the dynamics of elasmobranchs in the slough, bat rays do not appear to be any more residential than the other common elasmobranchs. In fact, the relative abundance of bat rays in the catch has increased steadily over the decades, which indicates that while their numbers may have declined, they may be less susceptible to habitat alteration or fishing pressure than leopard sharks or shovelnose guitarfish.

Elkhorn Slough is believed to function as a nursery area for a number of elasmobranchs. For coastal species, nursery habitats are usually located in productive shallow waters, such as bays or estuaries. These habitats are thought to be utilized as nursery areas due to abundance of prey, increased water temperatures, and lack of predators (Springer, 1967; Castro, 1993; Holland et al., 1993; Morrissey and Gruber, 1993; Simpfendorfer and Milward, 1993). Nursery areas can be further broken down into primary and secondary nursery areas (Bass, 1978). Primary nursery areas are where pupping occurs, while secondary nursery areas are utilized by neonates or juveniles for a period of time ranging from weeks to years.

Elkhorn Slough serves as a primary nursery area for bat rays (Barry, 1983; Talent, 1985; Martin and Cailliet, 1988a). This conclusion is supported by the fact that female bat rays were observed aborting pups during derby weigh-ins (Herald, 1953; King[3]) and near term fetuses were found during female dissections at derby weigh-ins (Herald et al., 1960). In addition, young-of-the-year bat rays were caught during the derbies.

The large number of immature animals caught during the derbies could also indicate that Elkhorn Slough serves as a secondary nursery area for this species. Elkhorn Slough is a highly productive environment with no significant predators which would make it an ideal place for small bat rays to utilize until they reach a large enough size to safely enter coastal waters. Talent (1985) found that small bat rays (<60 cm DW) were more common than larger rays during all seasons, though their abundance was lowest in the winter. This indicates that they use the slough as a secondary nursery area on a seasonal basis. It is likely that bat rays leave the slough in the winter when temperature and salinity decline, and return the following year once temperature and salinity increase


F

1950's	N = 245 Mean = 975.7
1960's	N = 110 Mean = 899.1
1970's	N = 176 Mean = 924.0
1980's	N = 112 Mean = 870.4
1990's	N = 51 Mean = 1049.2

M

1950's	N = 262 Mean = 949.4
1960's	N = 107 Mean = 882.4
1970's	N = 224 Mean = 845.4
1980's	N = 103 Mean = 871.5
1990's	N = 26 Mean = 883.1

Total Length (mm)
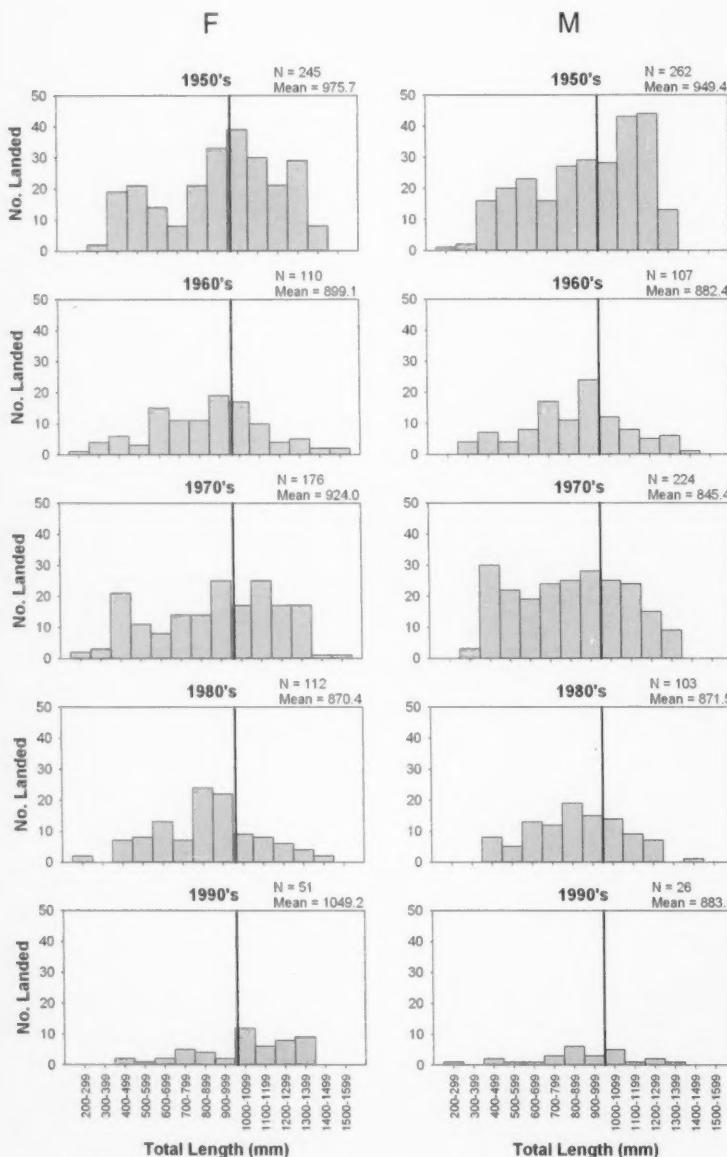
Figure 9.—Size class distribution of male and female leopard sharks by decade. The vertical line indicates size at 100% maturity.

[3]King, A. 1988. Peace Corps., Oakland, Calif. Personal observ.

as was found by Hopkins and Cech Jr. (2003) in Tomales Bay.

The role of Elkhorn Slough as a nursery area could also explain the difference between mature and immature sex ratios of bat rays. The nearly even sex ratio of mature bat rays is likely attributable to the reproductive seasonality of mature bat rays. Bat rays give birth in the late spring and summer and mate soon after giving birth (Talent, 1985; Martin and Cailliet, 1988a). The majority of derbies occurred in June, which would be near the end of their pupping period. If fertilization occurs shortly after pupping, as is suspected, one would expect there to be a sex ratio close to 1:1 at this time. In several bays along the coast of California and Baja California, Mexico, adult females greatly outnumber males during the spring and early summer, but the sex ratio evens out during the summer when males enter these areas to mate, at which point the sex ratio is around 1:1 (Ebert, 2003). It is likely that same pattern is occurring in Elkhorn Slough.

The sex ratio of immature animals heavily favored females and could be due to sexual segregation, which is well documented in elasmobranchs (Ripley, 1946; Springer, 1967; Myrberg and Gruber, 1974; Pratt, 1979; McKibben and Nelson, 1986; Klimley, 1987). Sexual segregation has been well documented in mature elasmobranchs. However, instances of immature elasmobranchs sexually segregating are not as common or as well known.

Ebert (2002) found that although male and female neonate and small juvenile broadnose sevengill sharks, *Notorynchus cepedianus*, utilize nursery areas in a similar fashion, juvenile females remain in nursery areas while adolescent males of a similar size leave. It appears as if this is related to size at maturity. Male broadnose sevengills reach maturity at a smaller size than females, and when they get close to maturity they leave nursery areas, while similarly sized females are still maturing and remain in nursery areas.

Klimley (1987) found that immature female scalloped hammerheads, *Sphyrna lewini*, moved into deeper waters at smaller sizes than males, and this move
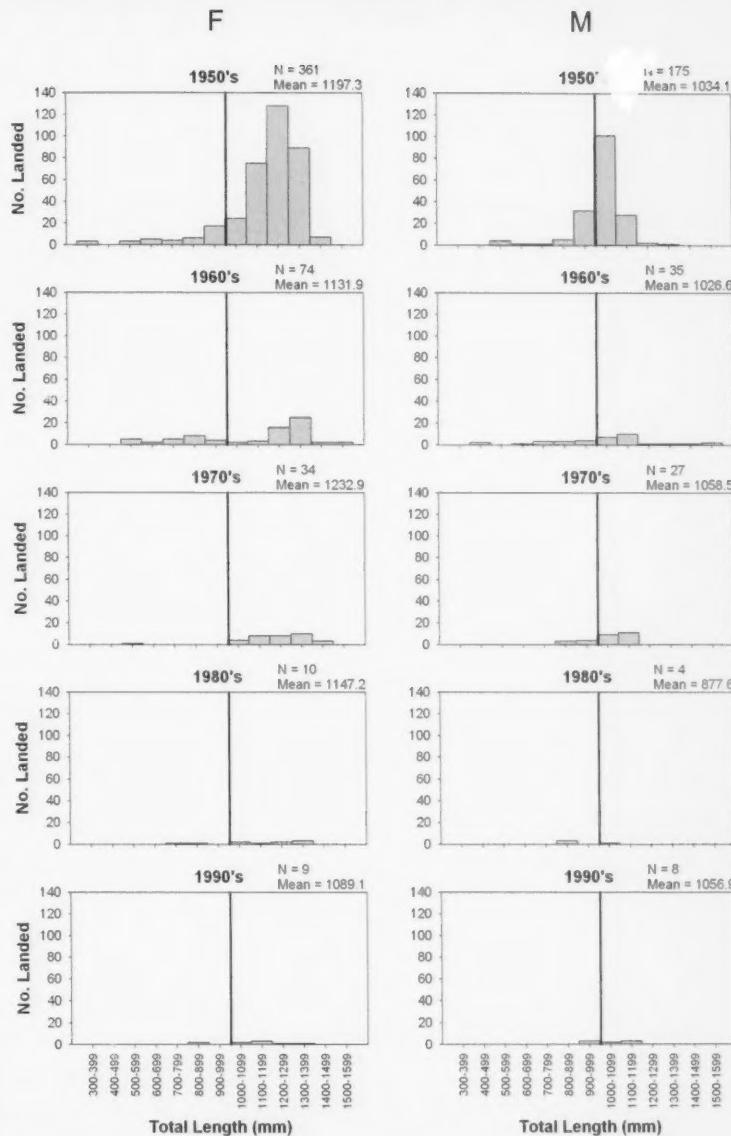

Figure 10.—Size class distribution of male and female shovelnose guitarfish by decade. The vertical line indicates size at 100% maturity.

resulted in an increased feeding rate. He theorized that by utilizing this different habitat, females were able to increase their growth rate and thereby reach maturity and attain a larger size more rapidly, which would allow them to increase their reproductive success. It is possible that bat rays are segregating by sex for a similar reason. Females mature at a larger size and attain larger sizes than males, so by utilizing the warm, prey rich and predator free waters of Elkhorn Slough as a secondary nursery area, immature female bat rays could increase their growth rates and reproductive success.
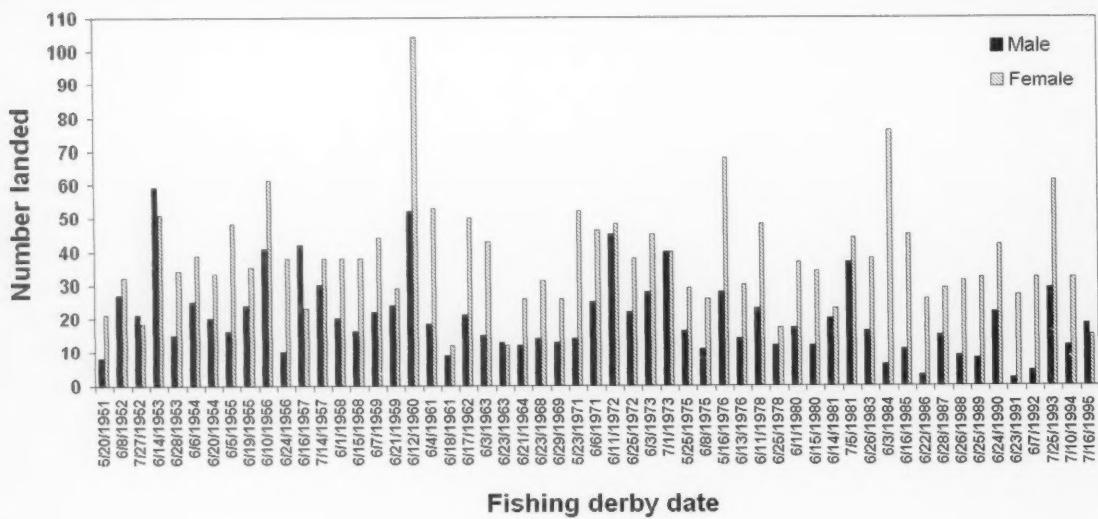
Figure 11.—Sex ratio of bat rays for each derby.
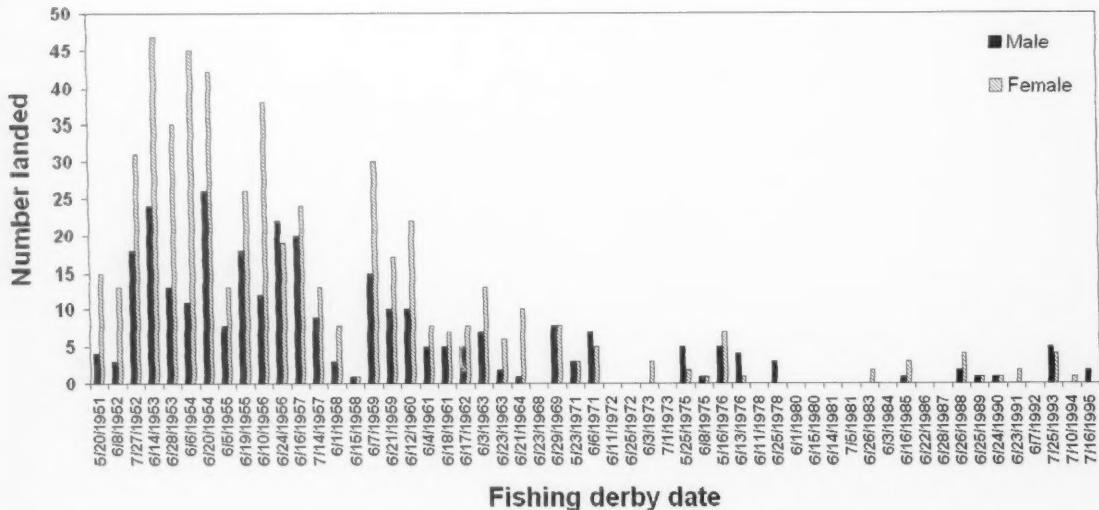
Figure 12.—Sex ratio of shovelnose guitarfish for each derby.

Leopard Sharks

Leopard sharks showed a similar pattern to bat rays in that the average number of leopard sharks landed per derby decreased in the 1980's and 1990's, and their relative abundance declined during that same period. It is unlikely that shifts in the oceanographic conditions would cause this, since Monterey Bay is in the middle of their range. It is more likely that any decline would be a result of other factors, such as habitat alteration or fishing pressure.
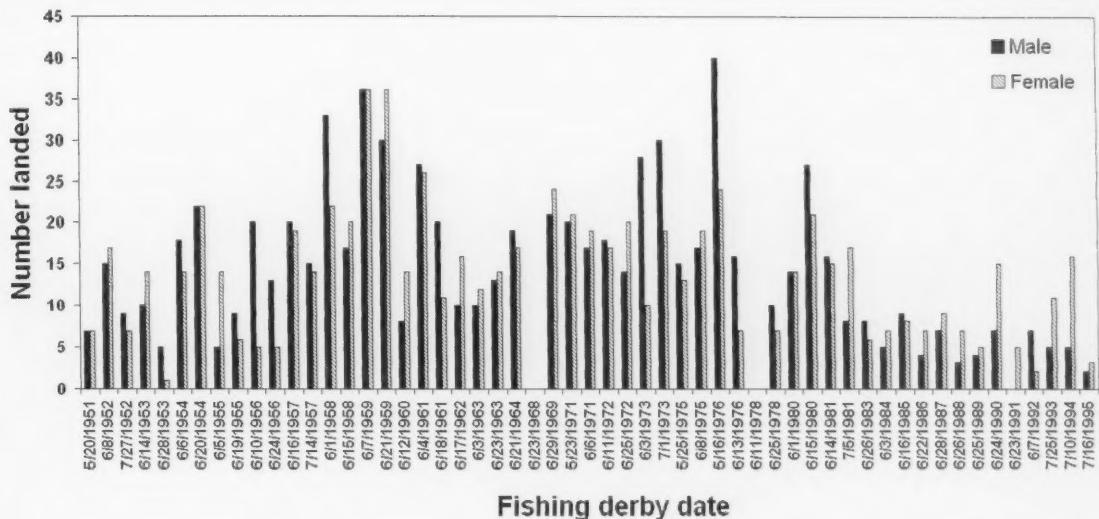
Figure 13.—Sex ratio of leopard sharks for each derby.

Habitat alteration likely played a role in any changes in leopard shark abundance. The diet of leopard sharks has been altered due to erosion, and possibly also to competition with sea otters (Kao, 2000). In addition, the type and amount of available habitat has changed, which likely has influenced patterns of habitat use. Habitat alteration has also likely impacted the nursery function of the slough as well as the tidal creeks that were used as nursery areas in the 1970's have been greatly altered (Barry, 1983).

In addition, the accumulation of agricultural pesticides and chemicals in the sediments of Elkhorn Slough (Phillips et al., 2002) could potentially impact leopard sharks directly through toxic effects or indirectly through impacting prey items (especially invertebrate infauna). This also may have played a role in the decrease in leopard shark abundance. Leopard sharks in Elkhorn Slough have been shown to contain significant concentrations of polychlorinated biphenyl (PCB) and organochlorine pesticide (OCP) contaminants (Vega, 1999), although how this affects their fitness is not known.

Another factor that could have impacted the catches of leopard sharks could be changes in regulations. A bag limit of three sharks and size limit of 36 inches was instituted in 1992. This could help explain a decline in the catch after that time, but the decline appears to have started in the early 1980's, so it cannot be attributed to new regulations alone.

The decline in the early 1980's could be due to the creation of Elkhorn Slough National Estuarine Research Reserve (ESNERR) in 1983. This created a large area that was off limits to fishermen, and ESNERR is heavily utilized by leopard sharks, especially during the spring and summer (Carlisle, 2006). This would not be surprising since leopard sharks use mudflats extensively and mudflats make up a large area of ESNERR (Carlisle, 2006). This could have effectively removed part of Elkhorn Slough's leopard shark population from fishing pressure from the derbies after 1983. This may also help explain the decline in bat rays in the 1980's and 1990's, as bat rays heavily utilize intertidal mudflats as well. The apparent decline in the abundance or catchability of leopard sharks in the 1980's and 1990's is likely a combination of these factors.

The proportion of the leopard shark catch that was mature varied from decade to decade, but the catch was always strongly dominated by immature sharks. Leopard sharks use the slough as a primary nursery area (Ackerman, 1971; Barry, 1983; Talent, 1985), and near-term females and young-of-the-year leopard sharks were caught during the derbies. However, the abundance of immature sharks indicates that like bat rays, leopard sharks also utilize the slough as a secondary nursery area.

Talent (1985) found that leopard sharks exhibited pronounced seasonal differences in their size class distribution, with the relative abundance of larger sharks (100+ cm) being greatest in the winter and spring and small and large sharks both being well represented in the summer and fall. While he was unable to sample very small leopard sharks due to the large mesh gill nets he used, the size class distribution of leopard sharks during the summer reported by Talent (1985) closely mirrors what was seen in this study. The lack of smaller sharks during the winter and spring indicates that the slough likely functions as a secondary, seasonal nursery area, much like in bat rays, with smaller sharks likely coming into the slough during the warmer months and leaving once the temperature and salinity drops (Hopkins and Cech Jr., 2003).

Similar to bat rays, the sex ratio of leopard sharks was likely due to reproductive seasonality. Both immature and mature leopard sharks had sex ratios that were relatively close to 1:1. However, the sex ratio of mature leopard sharks was often slightly more skewed towards females, especially in the 1990's when it was heavily dominated by females.

Leopard sharks give birth in the late spring-early summer, in particular during April and May, and they are likely fertilized shortly after giving birth (Ackerman, 1971; Talent, 1985; Ebert and Ebert, 2005). June is likely around the end of the pupping period and the beginning of the mating period, so one might expect that the sex ratio should be close to 1:1 at that time. The sexual segregation in immature leopard sharks is not nearly as dramatic as is seen in immature bat rays, indicating that both immature male and female leopard sharks are using Elkhorn Slough as a nursery area.

Shovelnose Guitarfish

The abundance of shovelnose guitarfish was very high in the early 1950's, but it declined steadily until they were only a very small component of the catch by the early 1970's. Shovelnose guitarfish are still caught in Monterey Bay and Elkhorn Slough but in low numbers. It is possible that the decline could be due to overfishing or habitat alteration. However, these options do not seem likely to be the principle causes of the decline. Their life history characteristics, which would be an indication of their susceptibility to overfishing, are similar to those of leopard sharks and bat rays (Ebert, 2003) which were abundant throughout the derbies, so it seems unlikely that they would be so strongly impacted by fishing pressure while the other species were not.

Habitat alteration should have increased the amount of habitat available to shovelnose guitarfish since they are commonly found in shallow soft bottom habitats such as mudflats (Ebert, 2003). A more likely explanation for the decline is that shovelnose guitarfish simply became less abundant in the Monterey Bay area due to a southern shift in their

distribution. The range of shovelnose guitarfish is typically reported as being from San Francisco Bay to the Gulf of California and possibly to Mazatlan, Mexico (Ebert, 2003), but they are most abundant in southern California. Herald and Dempster (1952) state that although the northern extent of the range of the shovelnose guitarfish is San Francisco, there are no authentic records of specimens north of Monterey Bay, so Monterey Bay is likely the northern limit of their range.

The relatively high abundance of shovelnose guitarfish in Elkhorn Slough in the 1950's could have been due to large-scale shifts in their distribution brought about by the Pacific Decadal Oscillation. Based on the records from the early derbies, it seems likely that there were more of them in the northern part of their range during the warm regime that occurred from 1925–46. As water temperatures cooled after the regime shift in 1947 it is possible that the thermal regime became less favorable to this warmer-water species and their numbers declined as their range shifted south. If this is the case, then the fishing pressure from the derbies may have hastened the decline of the species, since Elkhorn Slough was at the northernmost extent of their range, and their numbers may have been already declining. Their numbers declined north of Point Conception in general, not just in Elkhorn Slough. Data from the Recreational Fisheries Information Network (RecFIN[4]) shows that from 1980 (the earliest year on record in the database) to 2003 shovelnose guitarfish were almost completely absent from recreational fisheries north of Point Conception, but they were very abundant south of Point Conception.

In the southern extent of their range it also appears as if there was a shift in shovelnose guitarfish. In May 1974 in the Gulf of California off Guaymas, Mexico, the speckled guitarfish, *Rhinobatos glaucostigma*, and whitenose guitarfish, *R. leucorhynchus*, were abundant, but the shovelnose guitarfish was completely absent from the artisanal

fishery landings or shrimp trawl bycatch (Compagno[5]). However, shovelnose guitarfish are now the most abundant species of *Rhinobatos* off Guaymas (Márquez-Farias, 2002). This information from the southern end of their range combined with their decline north of Point Conception at the northern part of their range could possibly indicate that the range of shovelnose guitarfish may have shifted south, although this is speculative. If the range of the shovelnose guitarfish has indeed shifted south, why they have not shifted back north again during the warm regime from 1977 to the late 1990's remains an open question.

There is some evidence that shovelnose guitarfish used Elkhorn Slough as a nursery area. The majority of shovelnose guitarfish were mature, and females outnumbered males nearly 2 to 1, which could be indicative of the females using the slough as a nursery area. Bays and estuaries are known to be used as nursery areas by shovelnose guitarfish, and during their reproductive period their sex ratios can be highly skewed towards females in those areas (Ebert, 2003).

However, based on the very small number of immature animals caught, it is unlikely that Elkhorn Slough was an important primary or secondary nursery area for shovelnose guitarfish during the derbies. Small and young-of-the-year shovelnose guitarfish were caught on occasion, although not nearly as frequently as was observed in leopard sharks or bat rays. Based on what is known about the prey and foraging behavior of these species, it does not seem likely that small guitarfish would be more difficult to catch than small leopard sharks or bat rays, so it seems unlikely that the lack of small shovelnose guitarfish is due to gear selectivity.

Another possibility is that due to timing of parturition young of the year were not present during the time of year that the derbies occurred. In southern California they pup in the summer (Ebert, 2003), so if they were pupping

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[4]RecFIN http://www.recfin.org/

[5]Compagno, L. J. V. 2003. Checklist of Guaymas chondrichthyans. Shark Research Center, South Africa Museum. SRC report 2003-05-14, 4 p.

in Elkhorn Slough at the same time as in southern California young-of-the-year would likely be present in June. Talent (1985) only found eggs with little embryonic development in mature females and stated that there was no evidence that they use the slough as a nursery area. However, he sampled from 1971 to 1972 after their abundance had declined greatly, plus he primarily caught shovelnose guitarfish in the fall and winter when embryonic development would be less advanced if they pupped and mated in the summer.

Herald et al. (1960) observed that most of the adult females were carrying "eggs and embryos in their ovaries at the time of the derbies," which may suggest that shovelnose guitarfish may have used Elkhorn Slough as a primary nursery area during the early years of the derbies. However, Herald et al. (1960) argued that since so few very small shovelnose guitarfish were caught, it was unlikely that shovelnose guitarfish were giving birth in the slough. While it is possible that it was at one time a primary nursery area for the shovelnose guitarfish, there is no direct evidence from these data or the literature that Elkhorn Slough served as a nursery area from May to July during the time frame that the derbies occurred.

It is also possible that the age and sex structure of the shovelnose guitarfish catch is due to sexual segregation. Herald et al. (1960) suggested that they may segregate like the soupfin (or tope) shark, *Galeorhinus galeus*, which segregate by sex along the coast of California, with mature males being more common in northern California and mature females more common in southern California (Ripley, 1946). This type of segregation also occurs in the salmon shark (*Lamna ditropis*), where females are more common in the eastern Pacific and males in the western Pacific (Goldman and Musick, 2006). However, there is no evidence of this type of large-scale segregation occurring in shovelnose guitarfish.

Thornback

Thornbacks were very rarely caught during the earlier derby years, but during the late 1960's and 1970's their frequency of occurrence and abundance started to increase. This could be due to a northward expansion of their range. Currently, thornbacks range from Tomales Bay, Calif., to Thurloe Head, Baja California (Miller and Lea, 1972; Plant, 1989). As of the 1950's, thornbacks were reported as abundant south of Point Conception, and had only been found north of there on a few occasions (Starks, 1918; Walford, 1935; Herald, 1953; Herald et al., 1960), indicating that the few caught in the early years of the derby reflected the extreme northern extent of their range. While their numbers increased slightly until the end of the derbies in 1995, it is likely that this reflected their slow shift north and if data had continued to be collected it likely would have shown a sharp increase in the late 1990's.

Currently, thornbacks are one of the most abundant elasmobranchs in Elkhorn Slough (Carlisle[6]). Plant (1989) extended the northern range of thornbacks from San Francisco Bay to Tomales Bay based on thornbacks being caught in Tomales Bay in 1988, which was during a warm-water period of the Pacific Decadal Oscillation. He also reported an increase in the abundance of thornbacks caught around and north of San Francisco Bay and suggested that they may not be as uncommon as they were previously. RecFIN[4] data shows that thornbacks started appearing in the recreational catch north of Point Conception around 1994 and dramatically increased after 2000. All of this information indicates that the range of thornbacks has expanded northward, and this would account for their increase in abundance in the derbies during the later years.

Whether or not the concurrent decline in shovelnose guitarfish and increase in thornbacks in Elkhorn Slough are related is debatable. It is possible that the northward expansion of the thornback was facilitated by the decline of shovelnose guitarfish north of Point Conception. While shovelnose guitarfish were abundant in Elkhorn Slough, there were very few thornbacks caught, but once their numbers decreased to a very low level, thornbacks started being caught regularly and in increasing abundances. This is interesting since thornbacks and shovelnose guitarfish are of a generally similar ecomorphotype, so if shovelnose guitarfish were to be replaced by another species it makes sense that it would be by a species that fills a similar niche in the system.

Shovelnose guitarfish and thornbacks generally feed on similar prey items. Shovelnose guitarfish feed on crustaceans, bivalves, polychaetes, and teleosts (Roedel and Ripley, 1950; Talent, 1982; Eschmeyer et al., 1983; Love, 1996; Ebert, 2003) while thornbacks feed on crustaceans, molluscs, polychaetes, cephalopods, and teleosts (Feder et al., 1974; VanBlaricom, 1982; Ebert, 2003; Limbaugh[7]). Their overall ranges are similar and they also utilize similar habitats. Shovelnose guitarfish and thornbacks both occur primarily in shallow soft bottom habitats such as the mud and sandy bottoms of bays, sloughs, and coastal beaches (Roedel and Ripley, 1950; Dubsky, 1974; Feder et al., 1974; Eschmeyer et al., 1983; Larson and DeMartini, 1984; Ebert, 2003; Limbaugh[7]). However, these two distributional shifts could be purely coincidental and the lack of information on movements, patterns of habitat utilization, and competition between these species makes it difficult to draw any concrete conclusions.

The thornback catch was highly skewed towards females, which may indicate that the slough served as a nursery area or that sexual segregation was occurring. While data on their life history is lacking, Ebert (2003) states that they pup in the late summer and, if this is true, it could explain the dominance of females in the catch. They could follow a pattern similar to bat rays, where females enter bays and estuaries earlier than males to pup and males enter after pupping to mate with females.

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[6]Carlisle, A. Unpubl. data. Hopkins Marine Station, Stanford Univ., Pacific Grove, Calif.

[7]Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. Inst. Mar. Resour., Univ. Calif. La Jolla, IMR Ref. 55-9, 158 p.

Based on this model, May to July would be when females should be more abundant than males. However, although it is possible that thornbacks used the slough as a nursery area later in the year than the derbies occurred, there is no evidence that this actually occurred. It is more likely that the sex ratio observed during the derbies is due to sexual segregation. It is possible, however, that thornbacks currently use the slough as a nursery area. There is anecdotal information that gravid thornbacks have been caught in Elkhorn Slough in the last several years, but this has not been confirmed.

Round Stingray

Round stingrays were rarely caught during the shark derbies in Elkhorn Slough. Interestingly, most of the round stingrays were caught during the first half of the derbies. Although they are known to move north of Point Conception during periods of warm water, such as El Niño events (Babel, 1967), it is a more southerly species that is uncommon north of Point Conception.

Because they are more common in southern California, it is counterintuitive that they were caught primarily during the cool regime that lasted from 1947 to 1976. One possible explanation is that they used Elkhorn Slough as a thermal refuge, due to its warmer temperatures. This is a likely explanation since their distribution is strongly influenced by water temperature. They are more abundant in waters that are above 10°C, and are believed to aggregate in areas that experience increased temperatures (Babel, 1967; Ebert, 2003). Elkhorn Slough is significantly warmer than coastal waters during the summer, so it would not be surprising that round stingrays may be more abundant in the area. In addition, most of the round stingrays that were landed were caught near the thermal discharge from the Moss Landing power plant in the lower part of the slough, where water temperatures could be quite warm (Lea[8]). This is similar to what has been found in southern

[8]Lea, R. 2006. Calif. Dept. Fish Game (retired), Monterey, Calif. Personal commun.

California, where round stingrays have been reported to prefer warmer waters where thermal effluent from power plants is discharged (Hoisington and Lowe, 2005).

Another explanation for this pattern of abundance is that habitat alteration has decreased the amount of suitable habitat for this species. Round stingrays utilize soft bottomed habitat (Babel, 1967; Ebert, 2003), so the shift away from an unconsolidated soft bottom to a more consolidated clay bottom that has occurred since the 1970's may have reduced the value of Elkhorn Slough to the species. This change also could have impacted the availability of prey items, as has been demonstrated for teleosts (Lindquist, 1998) and leopard sharks (Kao, 2000).

The low numbers of round stingrays caught and the male dominated sex ratio indicate that round stingrays did not use Elkhorn Slough as a nursery area during the derbies and that they may segregate based on sex. Females move inshore to mate and give birth during the spring and summer in southern California (Babel, 1967). If they were pupping or mating in the slough, one would expect a sex ratio closer to 1:1. Talent (1985) did not catch any gravid females or juveniles, and believed that they did not breed in Elkhorn Slough. In this study, only 25% of the round stingray catch was measured, but they were all mature based on the maturity estimates from Babel (1967). They are known to segregate by age and sex with females living offshore in water deeper than 14 m, while adult males and juveniles occupy shallower habitats (Babel, 1967), which could explain the preponderance of males in the shallow slough.

Smoothhounds

The frequency of occurrence and relative abundance of smoothhounds increased starting in the 1960's. It is difficult to relate the increase in abundance in smoothhounds to temperature regime shifts because we have lumped together both brown smoothhounds, which have a more northern distribution, and gray smoothhounds, which have a more southern distribution (Ebert,

2003). Since the majority of smoothhounds caught in previous studies were gray smoothhounds (100% reported by Yoklavich et al. (1991); 77% reported by Talent, (1985); and 100% reported by San Filippo (1995)), it is likely that the smoothhounds caught during the derbies were mainly gray smoothhounds.

That the gray smoothhound has historically been the most abundant smoothhound species in Elkhorn Slough is curious since they are a more southerly species, and brown smoothhounds are one of the most abundant elasmobranchs in San Francisco Bay (De Wit, 1975; Ebert, 1986), which is geographically much closer. There was an increase in the frequency of occurrence of smoothhounds between the late 1950's and mid 1970's, which was during a cool regime, but it appears as if there is an even greater increase in smoothhound catch after the regime shift in 1977 to a warm regime. Sixty percent of the smoothhounds caught in the derbies were caught during this period of time. Assuming that most of the smoothhounds were gray smoothhounds, it is possible that the warmer water temperatures following the 1977 regime shift could have led to an increase in the abundance of this more southerly, warmer water species in Elkhorn Slough, although this is speculative.

San Filippo (1995) caught 312 gray smoothhound (71% of the catch) in 2 years of sampling between 1990 and 1992 in ESNERR. Only four smoothhounds were caught during that same time period in the derbies. This indicates that smoothhounds were more abundant in Elkhorn Slough during that period of time than the data from the derbies reveals, and suggests that the creation of ESNERR possibly led to shifts in the distribution and habitat use of smoothhounds and other elasmobranchs in Elkhorn Slough.

While sampling between early 2003 through late 2004 in ESNERR and the rest of the slough, only nine smoothhounds were caught (6 gray and 3 brown smoothhounds) (Carlisle[9]). Although

[9]Carlisle, A. Unpubl. data. Hopkins Marine Station, Stanford Univ., Pacific Grove, Calif.

different methods were used (Carlisle used gill nets, San Filippo used beach seines), this seems to indicate that their numbers have declined since the early 1990's. If the number of grey smooth-hounds has indeed declined, this suggests that their presence in the northern part of their range (i.e. Monterey Bay) is influenced by water temperatures. The period of highest smoothhound abundance appears to have been during the warm regime from 1977 to the mid 1990's, and their numbers appear to have declined after the PDO started to shift to a cold regime in the mid to late 1990's. The influence of temperature on gray smoothhound abundance is logical given that the northern extent of their range is Elkhorn Slough (Ebert, 2003).

Effects of the Derbies

It is hard to say whether or not the fishing derbies directly impacted the elasmobranch assemblage of Elkhorn Slough. Herald et al. (1960) theorized that the elasmobranch yield at an Elkhorn Slough derby was more an accurate reflection of the elasmobranch content of the slough on a particular day, rather than the number of fishermen participating in the derby, so smaller catch would indicate fewer elasmobranchs in the slough. The fact that the average catch decreased steadily over the decades and declined by 42% from the first decade to the last decade of the derbies despite a 50% increase in effort (number of fishermen) over the same period of time indicates that the size of the elasmobranch assemblage has declined.

CPUE data would be one way to examine the effect of the derbies, since CPUE calculated from a small area can be considered to be proportional to the local abundance (Maury and Gascuel, 2001). However due to the large gaps in the CPUE data it is difficult to directly address this question, although it still does provide valuable insight into the elasmobranch assemblage. Because the highest CPUE's (including the three large spikes in CPUE) all occurred during the early years of the derbies while the later years all had the lowest CPUE's, local overexploitation may have occurred since significant fishing

effort in a small area may tend to reduce local biomass and local CPUE (Fonteneau and Richard, 2003).

Whereas it appears as if the abundance or catchability of elasmobranchs in the slough has decreased over the years, it is impossible to directly attribute this to the derbies since other factors (e.g. regime shifts, habitat alteration, the creation of ESNERR) also contribute to the abundance and distribution of elasmobranchs. However, the derbies certainly had management and conservation implications. Given the limited size and semi-enclosed nature of the slough, the decline in CPUE with increasing numbers of fishermen indicates that the slough was likely getting "fished out" during large derbies. Herald (1953) suggested that the drop in bat ray catch from 59 in the 8 June 1952 derby to 39 in the 27 July 1952 derby might have been partially due to mortality from the earlier derby.

Despite significant fishing pressure, the number of elasmobranchs appeared to often rebound after the derbies, likely due to immigration of more elasmobranchs from coastal areas. This is demonstrated by the fact that in years when there were two derbies, at most a month apart, large numbers of elasmobranchs were usually caught in both derbies. If their numbers were not being replenished, one would expect the catch to always be less during the following derby, which was not always the case. At times the second derby actually had larger catches.

While the derbies at least temporarily depleted the number of elasmobranchs in the slough, the stability of the size class distributions in bat rays, leopard sharks, and shovelnose guitarfish (when present in significant numbers) indicates that neither fishing pressure from the derbies nor habitat alteration dramatically impacted the size or age structure of these three most abundant species. This also suggests that the populations of elasmobranchs in Elkhorn Slough are open populations with potentially high rates of immigration and emigration.

However, effectively managing elasmobranch populations is of great consequence given the important role that

they play in maintaining the overall health and stability of marine ecosystems (Bascompte et al., 2005). Because these species have late ages at maturity and low fecundity, they are vulnerable to overexploitation, and our knowledge of elasmobranch fisheries suggests a precautionary approach is warranted. Elkhorn Slough is the nursery area for a number of these species, and the derbies were occurring during the peak of their reproductive seasons, resulting in the killing of many gravid females. In addition to pregnant females, many immature animals were killed, and this can also have a large impact on the health of a population (Heppel et al., 1999). The cessation of the derbies was a positive event that will aid in the protection and management of local populations of elasmobranchs, which are an important component in local marine and estuarine ecosystems.

Summary

This study documents several shifts in the elasmobranch assemblage of Elkhorn Slough between 1951 and 1995, indicating that the elasmobranch assemblage of the slough is dynamic and responds to several factors. Possible reasons for these changes are the direct or indirect effects of habitat alteration, fishing pressure, and large-scale shifts in the oceanographic conditions, such as the Pacific Decadal Oscillation. Habitat alteration could influence the abundance of species by changing the amount and type of available habitat and the abundance and diversity of prey items. Whether it was habitat alteration, changes in the oceanographic conditions, or fishing pressure from the derbies that influenced the abundance of different species is difficult to say. It is most likely that the different factors worked in concert, but for different species, one factor may have been more important than the others.

The most notable change was the shovelnose guitarfish decline, which was possibly due to their range having shifted south, potentially as a result of the regime shift that occurred in 1947. This decline in shovelnose guitarfish coincided with an increase in the frequency

of occurrence and a slight increase in the relative abundance of thornbacks and smoothhounds. Thornbacks have since become one of the most abundant elasmobranchs in the slough, most likely due to their range having expanded northwards over the last several decades, possibly during the increased temperatures that occurred during the warm regime. The increase in smoothhounds was possibly a result of the increased water temperature that occurred during the warm regime.

Round stingrays were most common during the early years of the derby, possibly as a result of thermal refuging. They were very infrequently caught during the later years, possibly as a result of a decrease in the amount of suitable habitat. Bat rays steadily increased in relative abundance throughout the derbies, possibly due to habitat alteration increasing the amount of habitat suitable for bat rays, while the relative abundance of leopard sharks was fairly stable throughout the derbies, except for a slight decline during the 1980's and 1990's.

This study provides further evidence that Elkhorn Slough functions as both a primary and secondary nursery area for bat rays and leopard sharks. The sex ratios of bat ray, shovelnose guitarfish, thornback, and round stingray catch indicates that sexual segregation is occurring in these species in Elkhorn Slough. In immature animals this could be due to habitat or prey partitioning, and in mature animals it likely reflects reproductive seasonality.

It appears that the abundance of elasmobranchs in the slough declined during the course of the derbies, although it is difficult to attribute the decline directly to the derbies since other factors likely influenced elasmobranch abundance and distribution such as regime shifts, habitat alteration, etc. However, the derbies did appear to temporarily deplete the numbers of elasmobranchs in the slough, although they usually appeared to recover afterward. The cessation of the derbies has been beneficial to the health of the local populations of elasmobranchs, especially because Elkhorn Slough

plays such an important role in the life history of most of the elasmobranchs that utilize the slough.

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Nesting Success of Kemp's Ridley Sea Turtles, *Lepidochelys kempi*, at Rancho Nuevo, Tamaulipas, Mexico, 1982–2004

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Introduction

The Kemp's ridley sea turtle, *Lepidochelys kempi* (Fig. 1) is the most endangered sea turtle in the world with a dramatic decline attributed to egg exploitation and incidental capture in

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ABSTRACT—The Kemp's ridley sea turtle, Lepidochelys kempi, *was on the edge of extinction owing to a combination of intense egg harvesting and incidental capture in commercial fishing trawls. Results from a cooperative conservation strategy initiated in 1978 between Mexico and the United States to protect and restore the Kemp's ridley turtle at the main nesting beach at Rancho Nuevo, Tamaulipas, Mexico are assessed. This strategy appears to be working as there are signs that the species is starting to make a recovery. Recovery indicators include: 1) increased numbers of nesting turtles, 2) increased numbers of 100+ turtle nesting aggregations (arribadas), 3) an expanding nesting season now extending from March to August, and 4) significant nighttime nesting since 2003. The population low point at Rancho Nuevo was in 1985 (706 nests) and the population began to significantly increase in 1997 (1,514 nests), growing to over 4,000 nests in 2004. The size and numbers of arribadas have increased each year since 1983 but have yet to exceed the 1,000+ mark; most arribadas are still 200–800+ turtles.*

commercial shrimp trawls (NRC, 1990). Its population had been declining at an alarming rate since at least 1947, when an amateur filmmaker revealed an estimated 40,000 female Kemp's ridleys nesting on the beach in a single day (Carr, 1963).

This species is unusual and endangered because 1) it nests primarily on a single stretch of beach with it's epicenter at Rancho Nuevo, Tamaulipas, Mexico, (Fig. 2), 2) it nests primarily during the daytime and often in large aggregations called arribadas (Fig. 3), which makes it easier for egg collectors, and 3) the Kemp's ridley also has a coastal distribution that makes it particularly vulnerable to incidental capture in commercial fishing trawls.

Massive egg exploitation on the beach during the 1940's and 1950's severely curtailed recruitment of new turtles into the population, and, combined with an increasing mortality of adult and subadult turtles in commercial fishing trawls starting in the early 1960's, the population was dealt a devastating blow and reduced to a total of 706 nests by 1985 (Burchfield and Foley[1]). A description and review of the shrimp trawl mortality on sea turtles is presented by the NRC (1990). NOAA's National Marine Fisheries Service (NMFS) addressed the problem of incidental turtle bycatch (Fig. 4, 5) with the development of turtle excluder devices (TED's) to reduce incidental mortality of turtles

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[1]Burchfield, P. M., and F. J. Foley. 1985. Report on Republic of Mexico/United States of America conservation effort on behalf of Kemp's ridley sea turtles at Playa de Rancho Nuevo, Tamaulipas, Mexico, 1985. Available from the Gladys Porter Zoo, 500 Ringgold Street, Brownsville, TX 78520.

in commercial fishing trawls. A TED is basically a mesh grid inserted in a trawl that expels turtles from the net through a trap door (Fig. 6). A comprehensive review of TED development is provided by Watson et al. (1986).

In 1966, the Mexican Government (Instituto Nacional de Pesca) initiated a Kemp's ridley recovery program and began a research and conservation program near Rancho Nuevo. These efforts have concentrated on nest protection and increased hatchling production. In 1978, a collaborative program between Mexico and the United States (U.S. Fish and Wildlife Service) was developed to restore this species' population to a self sustainable level with the conservation efforts centered at Rancho Nuevo. Because this is the only place in the world where the large Kemp's ridley nesting aggregations occurred, it was declared the first National Reserve for the Management and Conservation of Sea Turtles in Mexico on 4 July 1977, when 13.2 miles (21.3 km) of beach were set aside (3.2 miles (5.1 km) north to 10 miles (16.2 km) south of Barra Coma). The Rancho Nuevo sanctuary was further expanded 10.6 miles (17 km) to the north (Barra Carrizo) in 2005. In 1981, the U.S. Fish and Wildlife Service contracted with the Gladys Porter Zoo in Brownsville, Tex., to administer the United States' field portion of the joint Mexico/U.S. effort to protect and increase the production of Kemp's ridley sea turtles at their natal beaches in the State of Tamaulipas, Mexico.

It is probable that the Kemp's ridley historically nested along the entire Gulf coast from Veracruz to Texas to some extent, and the early (1978–86) annual project reports support this with reports

Figure 1.—A Kemp's ridley turtle laying eggs during the day at Rancho Nuevo, Tamaulipas, Mexico. Photo by W. N. Witzell.

Figure 2.—The location of the main nesting beach at Rancho Nuevo, Tamaulipas, Mexico

of sporadic nesting along the entire Tamaulipas coast (Burchfield et al.[2]). As the turtle population began to increase, the number of turtle camps also increased and spread along the Tamaulipas coast to protect nesting activities (Fig. 7). The changes and development of the turtle camps is documented in a series of unpublished annual reports archived at the Gladys Porter Zoo, in Brownsville, Tex. (Burchfield et al.[2]).

From 1966 to 1978, conservation efforts focused on the area of Rancho Nuevo with the camp located first at Barra Calabazas and then at Barra Coma where it presently exists. In 1988, the program expanded to the south to Barra del Tordo with a camp at Playa Dos. In 1989 a third camp was established to the north at Barra Ostionales on Rancho Los Pericos in cooperation with the Tamaulipas State Government. The north camp's location was moved 6.2 miles (10 km) north of its original location, near to the town of Tepehuajes in 1996 for logistical reasons. In 1996, in coordination with the Tamaulipas' State Government, a camp was established in La Pesca. Additional camps have also expanded the project to the south to include the beaches of Ciudad Madero, Altamira, and, in 1997, the area of Lechuguillas, municipality of Vega de Alatorre, Veracruz.

The main strategy of these camps has always been to locate every nest and protect them in fenced corrals (Fig. 8). This controls egg predation from rac-


Figure 3.—An Arribada of several thousand Kemp's ridley turtles at Rancho Nuevo taken in the mid 1960's. Photo by R. Marquez-M.

[2]Burchfield, P. M. and various authors. 1978–2004. Published and unpublished annual reports on the Mexico/United States of America population restoration project for the Kemp's ridley sea turtle, *Lepidochelys kempi*, on the coasts of Tamaulipas and Veracruz, Mexico, var. pagin. Available from the Gladys Porter Zoo, 500 Ringgold Street, Brownsville, TX 78520.

coons, *Procyon lotor*; skunks, *Spilogale* sp. and *Mephitis* sp.; coyotes *Canis latrans*; ghost crabs *Ocypoda albicans*; and humans. Virtually all nests left in situ on the beach are depredated unless protected by wire enclosures. Egg harvest by local villagers was minimal until about 1997, when a combination of new roads and ranches were constructed that made beach access easier. Recent increases in arribadas have led to increased egg poaching as beach workers are often too busy to effectively cover the entire beach at once (Burchfield et al.[2]). The thieves wait in the dunes until the patrol has passed, and then intercept any turtles coming ashore to nest. Fortunately, these impacts remain minimal (e.g. 8 of 4,406 nests in 2004 were poached at Rancho Nuevo).

In this paper we document the apparent success of these conservation strategies using nesting data from the main camp at Rancho Nuevo collected from 1982 to 2004.

Material and Methods

The nesting data reported here were recorded at the main sea turtle Camp at Rancho Nuevo, Tamaulipas, Mex. Typically, there were three beach patrols a day where workers rode the entire length of the beach on four wheel all terrain vehicles. The first patrol was usually at sunrise, the second patrol at 1100 h, and the third patrol at 1500 h. More patrols were sent out if ridleys were expected and all camp personnel and vehicles were dispatched if there was an arribada. Patrol times and nesting beach protocols have varied between seasons and within seasons depending on turtle density, staffing, status of vehicles, and policies of the camp managers.

Turtles that were encountered were checked for flipper and passive integrated transponder (PIT) tags. If there were none, the appropriate tags were then applied if the equipment was available, the turtle measured over the carapace from the tip of the left first marginal scute to the tip of the right post central scute, and the nests marked for relocation to a protected corral. Nests were then collected in woven plastic bags as soon as possible, counted, and transferred to the corral area for reburial (Fig. 8). This entire process from nesting to reburial took between 1 to 12 hr, depending on the number of turtle nests and the staffing at the camp. Data sheets were filled out for each nest and they recorded date
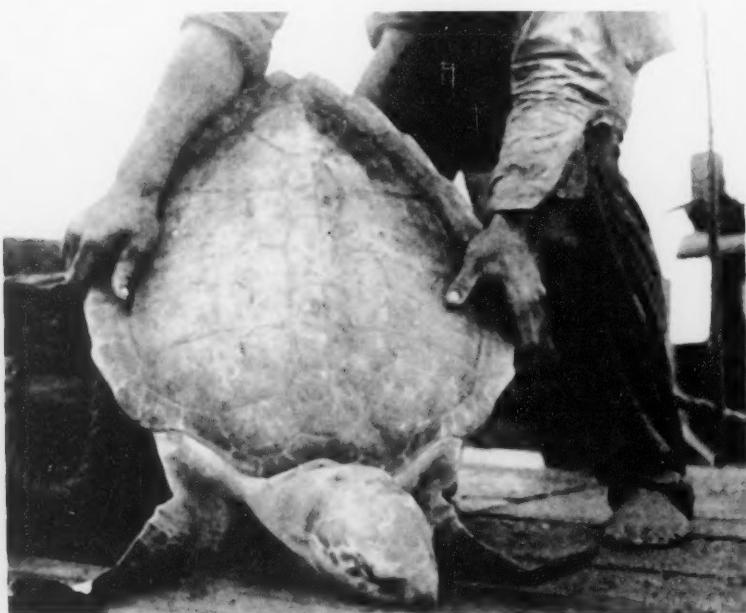

Figure 4.—A large Kemp's ridley turtle (locally called a white turtle) on the deck of a Louisiana shrimp boat in the early 1920's. Photo from La. Dept. Fish. Wildl., provided by C. Caillouet.

Figure 5.—A sea turtle on the deck of a trawler with the usual finfish bycatch. Photo by L. Ogren.

and time, location of nest on beach, and number of eggs.

Holes were dug in the corrals to a depth of 17.8 inches (45 cm) with posthole diggers and a bell-shaped nest cavity was carved by hand to resemble a natural nest in terms of depth, shape, and size (Witzell, 2005). The eggs were deposited into the resulting hole and the data sheet further recorded time of reburial. The nests were then surrounded with a circular mesh enclosure to capture the hatchlings when they emerged.

Hatchlings typically emerged after 45–55 days (usually at night) and were immediately collected, counted and taken to the beach at random sites located 0.5–1.8 mile (1–3 km) north and south of the hatchery, for release on the beach front (Fig. 9). These release sites were arbitrarily selected by the persons releasing the hatchlings and no effort was made to spread the hatchlings over the entire beach or the area where the nests were actually collected. The hatchlings were attended until they have traversed the sand and have successfully reached the water. Those hatchlings that emerged during daylight were held in a cool dark room and released that night.

Results and Discussion

The Kemps ridley sea turtle is primarily a diurnal nesting species, with most nesting taking place during the late morning or afternoon hours, and basic reproductive information has recently been collected on the beach at Rancho Nuevo. These data, published by Witzell et al. (2005), were compared to data collected in the 1960's and the results of the recent study are summarized here. It is interesting to note that the sizes of the nesting turtles, eggs, and egg clutches were smaller than originally recorded in the 1960's, suggesting that there is now a younger nesting population. The mean length and weight of recent nesting females was 25.8 inches (65.5 cm) and 77.6 lb (35.2 kg), the mean clutch size was 100.7 eggs, the mean incubation period was 50 days, and the mean internesting interval is 24.4 days. The turtles are capable of nesting three times per season, with an average of 1.8 years between nesting seasons.
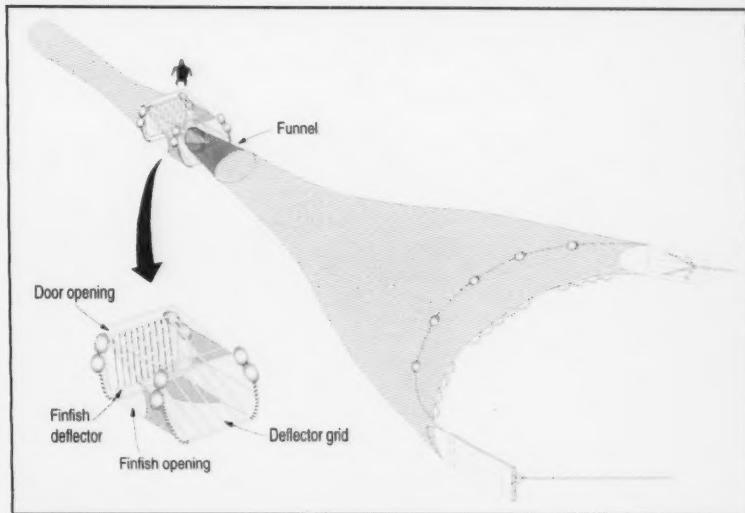

Figure 6. —Schematic diagram showing how a turtle excluder device (TED) works. Illustration provided by J. Watson.

Figure 7.—Kemp's ridley sea turtle research and conservation camps along the Mexican coast.

Juvenile turtles spend up to two years in the pelagic environment before settling out into distinct coastal areas feeding on invertebrates (Witzell and Schmid, 2004; 2005) until they approach maturity. These are very specific

areas and are commonly referred to as developmental habitats. The turtles stay in these areas from about 7.8 inches (20 cm) to 21.6 inches (55 cm), when they move offshore into deeper water (Ogren, 1989; Collard and Ogren, 1990;

Figure 8.—Eggs collected at Rancho Nuevo are transplanted into protected corrals. Photo by W. N. Witzell.

Figure 9.—Hatchling Kemp's ridley turtles released on the beach at Rancho Nuevo. Photo by J. M. Witzell.

Witzell and Schmid, 2004). Several minor coastal developmental habitats are located along the eastern coast of the United States from Cape Cod Bay, Mass., to Cape Canaveral Ship Channel, Fla., but the most important developmental habitats are in the in the Gulf of Mexico. The coastal waters of the Texas–Louisiana border and the Cedar Keys area of northwest Florida are two such developmental habitats, but the Ten Thousand Islands of southwest Florida is possibly the largest and most important developmental habitat in the Gulf of Mexico (Witzell and Schmid, 2004). The young turtles remain in these coastal habitats for about 8–10 years before maturing at approximately 11–15 years of age, 22 inches (56 cm) long (Schmid and Witzell, 1997) and returning to Tamaulipas to breed. Immature turtles from as far away as the U.S. middle Atlantic coast were once believed to have been 'lost' from the nesting population but tagging has shown that these turtles also return to Mexico to breed (Witzell, 1998). Nesting turtles may move considerable distances between nesting sites and have been recorded nesting at the Padre Island National Seashore in Texas and subsequently nesting at Rancho Nuevo within a nesting season (Witzell[3]).

The main nesting season at Rancho Nuevo typically occurs from April through June, with some nesting extending into July (Table 1). May is the month when most of the arribadas (defined here as at least 100 turtles per daily event) occur with April and June being second and third respectively (Fig. 10). The nesting season in two recent years (1998, 2001) began in March and extended into August. Additionally, significant numbers of turtles nested at night in 2003, and we believe that the extended nesting seasons and the night nesting might be indicators of an increasing population.

[3]Witzell, W. N. 2004. Observations of special interest. *In* Report on the Mexico/United States of America population restoration project for the Kemp's ridley sea turtle, *Lepidochelys kempi*, on the coasts of Tamaulipas and Veracruz, Mexico, p. 25. Available from the Gladys Porter Zoo, 500 Ringgold Street, Brownsville TX 78520.

The total number of nests and the numbers of arribadas at Rancho Nuevo can be used as indices of conservation success. Although these numbers are generally increasing (Fig. 11), there is one environmental parameter that can affect nesting density on this beach section. Nearshore currents can affect the nesting density and location of nesting activity on any section of the beach. For instance, there was a very strong (1–3 km/hr) northerly current during the 2000 nesting season (Witzell, personal observ.). This displaced the turtles to the northern section of Rancho Nuevo and a large portion of the Rancho Nuevo turtles to the Tepehuajes camp. This displacement could affect the nesting numbers recorded at Rancho Nuevo on any given year. Since nesting numbers have traditionally indicated to conservationists how successful recovery efforts were progressing, unnoticed lateral nesting displacement could give false impressions of recovery success between successive years.

There were few distinct arribadas consisting of 100+ turtles from 1982 to 1996, most turtles nested individually or in small groups. It is interesting to note that there were two 100+ turtle arribadas even in 1985, the year with the lowest recorded number of nests at Rancho Nuevo (706), and we cannot account for this. From 1978 to 1996 the number of 100+ turtle arribadas ranged from 0 to 4 (with 1987 having no arribadas) and there were 26.1 days between events (SD = 7.7). However, as the population started to increase (Fig. 11), the numbers of arribadas per year has increased from 5 in 1997 to 11 in 2004. Unlike the earlier events (1978–96) with a mean 26.1 days between events, the recent events are likely to occur less than 10 days apart and many 1–3 days apart. This indicates that either an arribada had taken place over a 1–3 day period and/or there were more than one group of turtles nesting (arribadas 3–10 days apart). It is difficult to discern individual arribada events after 1996 because of their frequency, and it appears that the turtles are beginning to form into different groups that produce multiple arribadas
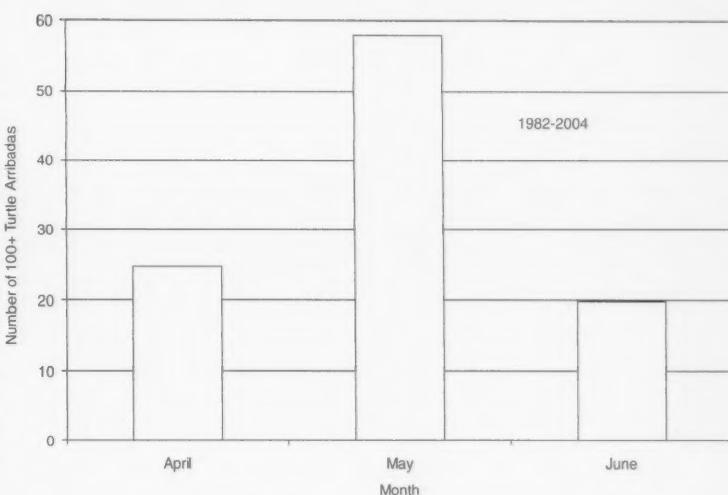

Figure 10.—Seasonal distribution of 100+ Kemp's ridley turtle arribadas.

Table 1.—Nesting season, by year, at Rancho Nuevo: X= 50+ nests, O= less than 50 nests.

Year	March	April	May	June	July	August	Total Nests
1982		X	X	X	X		792
1983		X	X	X	O		862
1984		X	X	X	O		924
1985		X	X	X	O		706
1986		X	X	X	O		742
1987		X	X	X	X		737
1988		X	X	X	O		854
1989		X	X	X	X		739
1990		X	X	X	O		780
1991		X	X	X	O		840
1992		X	X	X	O		899
1993		X	X	X	X		857
1994		X	X	X			1,153
1995		X	X	X	X		1,430
1996		X	X	X	X		1,288
1997		X	X	X	X		1,549
1998	O	X	X	X	O	O	2,413
1999	O	X	X	X	O		2,298
2000	O	X	X	X	O		3,778
2001	O	X	X	X	X	O	3,846
2002	O	X	X	X	X		4,194
2003	O	X	X	X	X		5,380
2004	O	X	X	X	X		4,463

as the population continues to build. There is a tendency for mass nesting to occur on windy days (Witzell et al., 2005), but it is typically windy each day on the Tamaulipas coast during the nesting season. Arribadas were observed on both calm and windy days as well as during thunder storms.

The population was slowly building during this period (1982–96) but it was apparently incapable of forming large

nesting aggregations with so few animals. The average number of 100+ turtle arribadas per season during this time period was 2.4. However, there were five arribadas in 1997, one of which was over 400 turtles. This was the first 400-turtle arribada since the Bi-National Program was initiated in 1978 and it marked the year that the ridley population started to increase. As the population increased, the average number of 100+

turtle arribadas per season (1997–2004) increased from 2.4 to 8.6, and there was evidently more than one group of individuals forming the aggregations. It is also during this time (1997 to 2004) that 200+ turtle arribadas became more common, and we expect the first 1,000 turtle arribada soon.

It is difficult to say how these nesting patterns will progress as the population continues to recover. Historically, there are no data available on daily nesting prior to the population crash so it is unknown whether the turtles will eventually join into one massive nesting aggregation, or stay separated into several groups, as appear to be happening now. The increase in yearly nesting of Kemp's ridley turtles since 1982 clearly shows the success of this Bi-National recovery project. The recovery continues to escalate as more turtles form multiple arribadas, which will hopefully soon be in the thousands. It is imperative that the beach conservation effort continues to protect every nest until the population can sustain natural depredation on eggs and hatchlings. It is also imperative that refinement and mandatory use of TED's for all commercial fishing trawls continues.

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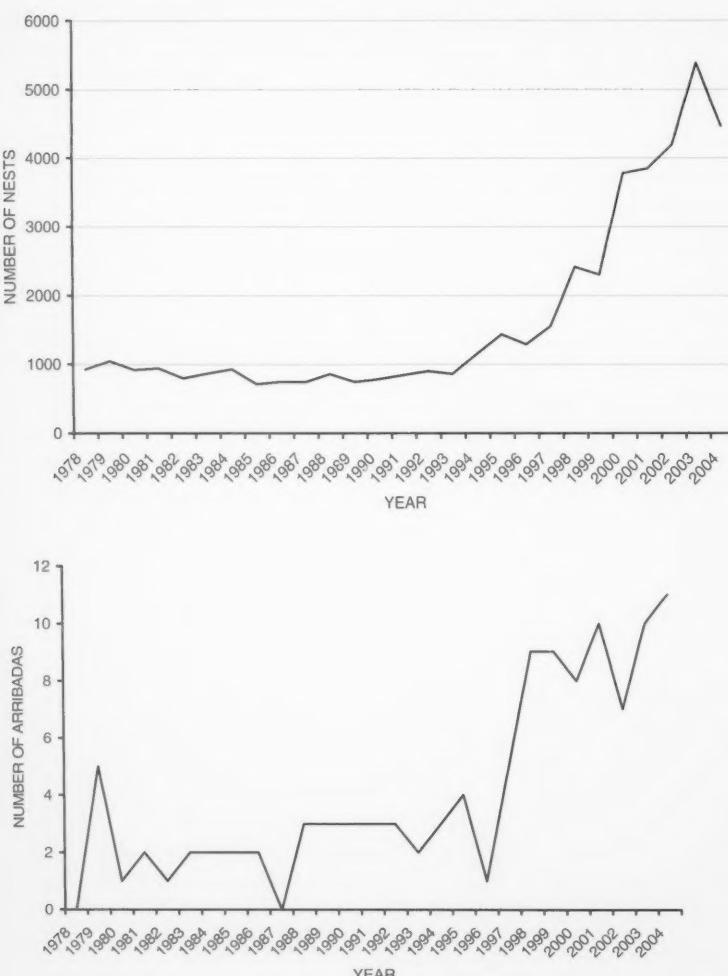
Figure 11.—The total number of nests recorded at Rancho Nuevo and the numbers of 100+ Kemp's ridley turtle arribadas, (1978–2004).

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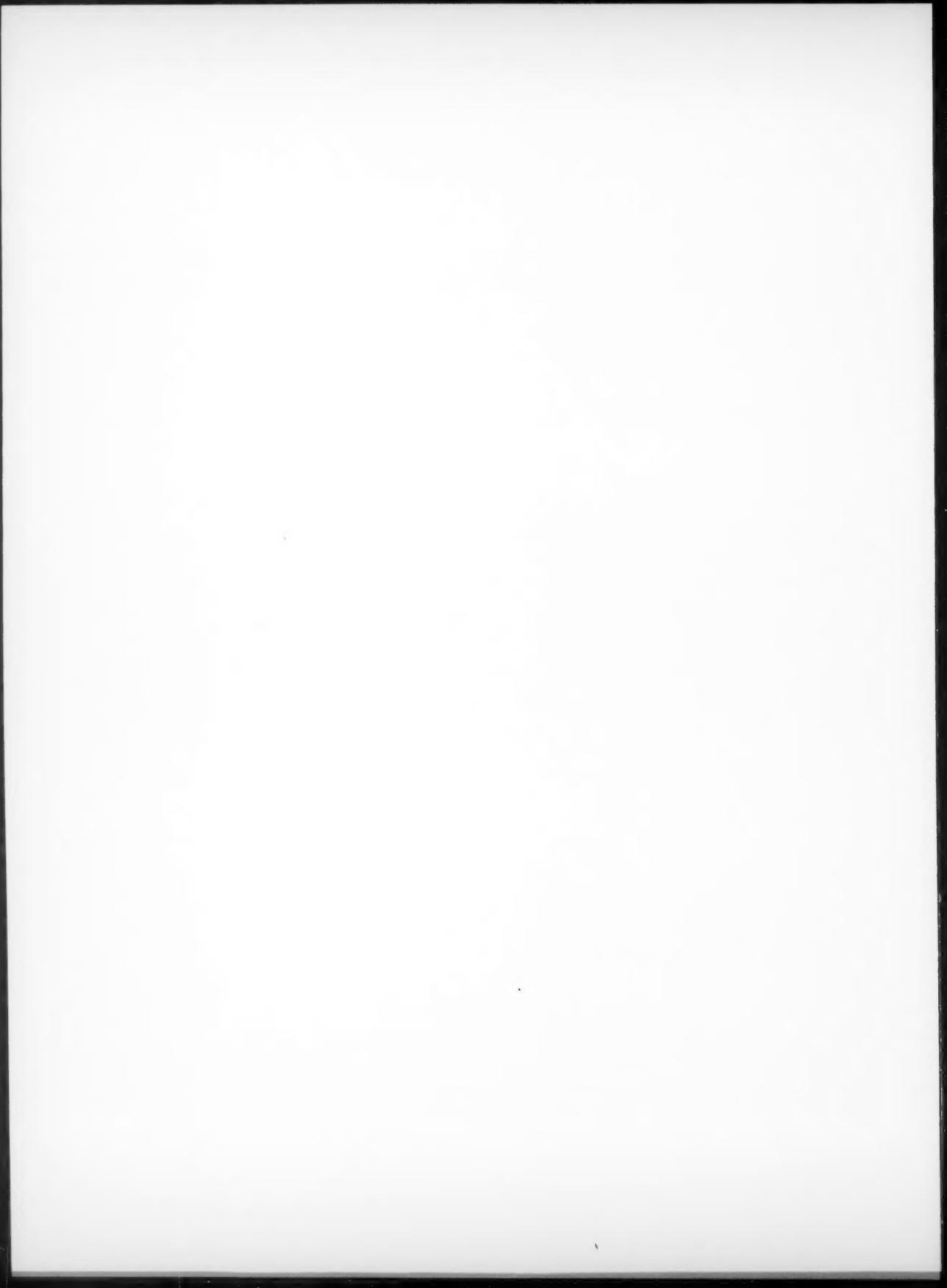
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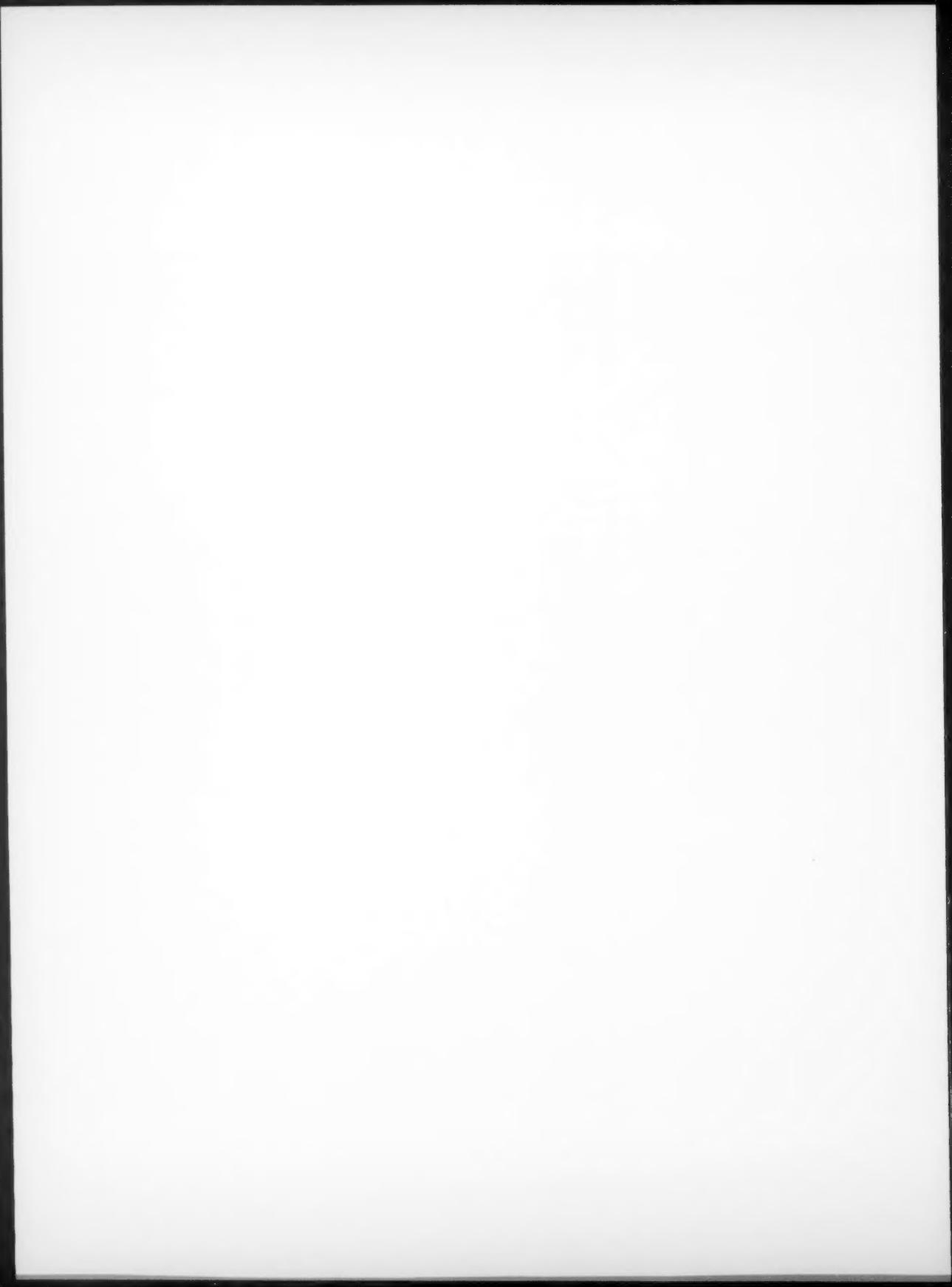
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